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MEIOTIC ABERRATIONS AND STERILITY IN ALOPECURUS MYOSUROIDES HUDS.

BY *HELGE JOHNSSON*
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I. INTRODUCTION.

SEVERAL investigators have dealt in more or less detail with the cytological behaviour of various species belonging to the gramineal genus *Alopecurus*. Somatic chromosome numbers, for instance, have been determined by MARCHAL (1920), KATTERMANN (1930), AVDULOV (1931), FLOVIK (1938), STRELKOVA (1938), and JOHNSSON (1941). Studies of meiosis have been published by CHURCH (1929), RANCKEN (1934), FLOVIK (1938), and JOHNSSON (1941). The relation between chromosome number and geographical distribution has been treated by STRELKOVA (1938), while JOHNSSON (1941) has described the cytogenetics of a number of artificial species hybrids.

Through these investigations a not inconsiderable knowledge of the cytogenetical structure of the genus has been gained. The chromosome numbers within the genus are built up on the basic number 7. Diploid, tetraploid, octoploid, decaploid, and approximately 16-ploid species occur. The total area over which the genus is distributed extends over practically the whole of the frigid and temperate zones of the northern and southern hemispheres. The diploid and tetraploid species, OVEZIMNICOV's (according to STRELKOVA, 1938) groups *Annuae*, *Pratensae* and *Ventricosae*, cover the greater part of the range and are especially bound to the damper meadow lands of the lowlands. The octoploid species constitute a taxonomically and geographically well defined group, the group *Vaginatae* (OVEZIMNICOV), which has its chief range in the mountainous regions of West Asia. The high-chromosomal species, finally, occur along the coasts of the Polar Seas, both the Arctic and Antarctic.

The diploid and tetraploid species represent two types with regard to chiasma morphology. At I—M one type has completely terminal chiasmata, the other is entirely non-terminalizing. In the tetraploid species quadrivalents occur in low frequency, and in the high-chromosomal there is some multivalent frequency. Some species hybrids are spontaneous, and after artificial pollination the species hybridize more

or less readily in many combinations, even when there are great differences in chromosome number and geographical origin. Hybrids have been obtained, for instance, between the 28-chromosome *A. pratensis* of Sweden and the 112-chromosome *A. antarcticus* of Tierra del Fuego. A characteristic feature of some triploid hybrids is that their trivalent frequency is far greater than the quadrivalent frequency of the tetraploid parent species. The facility with which species hybrids are obtained, and the frequently high degree of syndesis shown by them, have been interpreted by JOHNSSON (1941) as an indication that there is an essential degree of homology between the gross structures of the chromosomes within the genus. The cause of the low frequency of multivalents in the polyploid species is considered by the same observer to lie in a genotypically conditioned tendency to bivalent formation.

The present work relates exclusively to *A. myosuroides* HUDS. and is an attempt to inquire further into the cytogenetics of one of the diploid species of the genus, which to a certain extent may be considered to represent the original species of this high-polyploid genus.

It is a very great pleasure for me to have this opportunity of tendering my most sincere thanks to my teachers of genetics at the University of Lund, Professor Emeritus H. NILSSON-EHLE and Professor A. MÜNTZING. At the same time I would express my cordial thanks to Dr. Å. GUSTAFSSON and Dr. A. LEVAN for their kindness on many occasions in giving me pointers to the literature and other valuable advice. The present work has been carried out in its entirety at the Institute for the Breeding of Forest Trees, to the Director of which, Professor N. SYLVÉN, I am very greatly indebted for the privilege accorded me of utilizing the resources of the Institute for this theoretical investigation, as well as for the personal interest and kindness he has always shown me. I am also indebted to Miss ASTRID MELIN and Miss GUDRUN NILSSON for valuable technical assistance.

II. MATERIAL AND METHODS.

The plant material underlying the investigation was originally raised from seed that was obtained through the mediation of the Lund Botanical Garden from the botanical gardens of Delft, Lyons, Nancy, Rouen, Liége, Tashkent, Brunn, Brussels, Tabor, München, Paris, Rennes, and Jena. Some material from an unknown source denoted 47x is also included. The different populations raised from these sources are denoted in the following text by their origin.

The self and cross pollinations were carried out in the spring of 1941 in pollen-proof isolation boxes in the greenhouse. During the following vegetative periods isolation by distance was used when performing these operations, the parental plants being planted at least 30 metres apart at the edge of a large field. As each isolation unit did not comprise more than one or two plants, this distance was considered satisfactory. No spontaneous population of the species was in the vicinity, contamination by foreign pollen being therefore excluded.

The pollen evaluations were made in aceto-carmine + glycerine preparation, as a rule on one specimen from each plant. Ten visual fields (magnification 30 × 7) of each specimen were counted. On an average about 75 pollen-grains occurred within one visual field. The percentage for each visual field was computed and the means of the ten visual fields calculated. The accuracy of the comparisons between the means has been determined for an arbitrary page of the report taking up ten determinations, the results being as follows:

Per cent. good pollen: 67,1; 74,8, 80,4, 54,5, 57,0, 85,8, 77,8, 61,7, 72,9, 52,1.

Analysis of variance:

	Degrees of freedom	Sum of squares	Mean square	Standard deviation
Between slides (plants)	9	13.001,54	1.444,62	—
» visual fields (within slides)	90	6.478,50	71,98	8,48

The significance of the differences between specimens (plants) is thus placed beyond all doubt. The standard deviation for a visual field is 8,48 %, i. e. for the mean of ten visual fields 2,68 %. A difference between the percentages of good pollen of two plants that amounts to about 8 % and above can thus be considered significant.

The pollen character in a certain plant, however, may be conceived as varying owing to modificative influences (weather), and undoubtedly does so occasionally. Still, in all cases when pollen samples were taken from the same plant on different occasions very accordant values were obtained. Pollen specimens from one plant, for instance, gave on three occasions 67,1, 72,1, 72,9 %.

For fixing root-tips as well as PMC's diluted chrome-acetic acid formalin was used. At the PMC fixations the right stage was first

ascertained in aceto-carmine preparation, in addition to which pretreatment in Carnoy's fluid was employed.

The drawings were made with the aid of Abbe's drawing apparatus, as a rule with a 100 × objective and a 15 × or 30 × eyepiece. The photomicrographs were taken with a Zeiss spherolux camera on Agfa microplates. Further particulars as to methods are given in the course of the work.

III. SOMATIC IDIOGRAM.

At mitosis the chromosomes of this species, like those of all other *Alopecurus* species, are long and flexible (Fig. 1).

The length of the seven pairs are respectively 8,4, 6,4, 5,4, 5,0, 4,4,

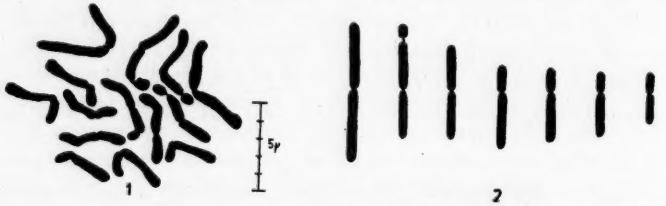


Fig. 1. Somatic chromosome plate of *Alopecurus myosuroides*. × 2200. — Fig. 2. Diagram of the somatic chromosomes.

3,8 and 3,0 μ. These dimensions are means of ten metaphase plates especially well suited for measuring. Especially conspicuous is the occurrence of a chromosome pair that is markedly longer than the rest. The length of the other pairs fall fairly uniformly down to the shortest, which is a little more than one-third the length of the longest pair. The centromeres are median and submedian, median in the three longest pairs and in the shortest pair, submedian in the rest. In the longest pair but one a secondary constriction is mostly observed that cuts off a satellite, the length of which approximates the chromosome breadth. Occasionally secondary constrictions also occur in the other chromosomes. Fig. 2 illustrates the situation in diagrammatical form. Positive identification of the different chromosome pairs is impossible for the following reasons:

(1) The chromosomes are overlong for the lumen of the cell (diameter of the spindle) and are hence mostly more or less curved and coiled.

(2) The chromosomes appear to vary in length rather considerably from cell to cell.

(3) Secondary constrictions do not occur regularly, and nor is it always possible to determine the exact position of the centromeres.

Other fixatives may give better specimens for morphological observations of the chromosomes. Tests with osmic-acid fixative, however, have not given good results.

IV. NORMAL MEIOSIS.

At I—M there are rod-shaped bivalents with one chiasma as well as ring-shaped ones with two chiasmata. The number of rings per PMC in 200 cells was:

Number of rings	0	1	2	3	4	5	6	7	Mean
Number of PMC's	0	0	13	29	66	65	26	1	4,33

The distribution of PMC's with different numbers of rings is binomial, and all chromosome pairs form ring-bivalents in the same

3

Fig. 3. The seven bivalents of one PMC, separately drawn. × 3000.

frequency (JOHNSSON, 1941). Thus, the chiasmata frequency at I—M is not correlated to the chromosome length. The mean number of chiasmata per bivalent is 1,62. The variation in chiasmata frequency between different normal plants seems to be insignificant. As a rule, the chiasmata are interstitial, only rarely is a completely terminal chiasma seen (Fig. 3). As seen in the figure, the segments between the chiasmata and centromeres are often filiformly drawn out, especially in the short chromosomes. This must mean that the chiasmata are especially resistant to the tension produced by centromere repulsion. Consequently, the anaphase separation does not seem to admit of being explained solely by an increased tension, but there must presumably occur some internal alteration or other of a nature to abolish the attraction between the paired chromatids. This is evident from the fact that anaphase separation has not the character of a continued termin-

alization; instead, the chiasmata open as a result of the paired chromatids separating simultaneously along their whole length. The X-form of the chromosomes during the later stage of anaphase also indicates that the chromatids are then repelling one another. Thus, anaphase separation does not seem to be explicable, in any case solely, on the basis of the attraction that arises between poles (centrosomes) and centromeres (DARLINGTON's interpretation), but parallel with this an internal chromosome alteration must be assumed to occur. The situation in reality seems to be that metaphase is broken off by an internal chromosome change, whatever the nature of this change may be.

The later phase of meiosis has the usual, well-known course and leads to the development of regular tetrads.

V. MEIOSIS IN THE TETRAPLOID CONDITION.

In order to enable the course of meiosis to be studied in the tetraploid condition a number of colchicine treatments have been carried out. The material used for examination was seed from two self-pollinated I_2 plants. One of the plants belonged to a $\pm$ normal family originating from Paris, the other was a family originally coming from Rouen and was abnormal in certain cytological respects. In this section only the normal offspring will be discussed, while those showing deviations will be dealt with later.

The colchicine treatment was applied by two different methods. In one the seed was allowed to germinate on filter paper moistened with 0,1 % colchicine solution and was kept on the paper for two weeks. In the other method the seed was allowed to germinate on filter paper moistened with distilled water until the coleoptiles were about 3 mm long, after which the seedlings in their entirety were submerged in 0,1 % colchicine solution for 24 hours. The result with regard to the 2n number in the root-tips and to the pollen quality is given in Table 1. The method of treatment denoted as »S» implies submersion in colchicine solution, while that with continuous germination on filter paper dampened with colchicine solution has been denoted as »G». The submersion method proved to be decidedly superior. All the plants treated by this method were tetraploids in the root-tips, while the long-term treatment gave mixoploid or unaffected plants. The mortality following submersion was also substantially lower than that after long-term treatment. Although the root-tips proved to be extremely tetraploid, the pollen of a number of plants, e. g. plants 8—9—1 in the table, could be

normal, with a diameter of about 14 units. In other plants, again, the pollen was of quite a different order of size. To exemplify this category plants 8—9—2 have been included in the table. The pollen diameter is here about 18 units compared with 14 in untreated plants, e. g. plants 8—13. Fig. 4 *a* shows pollen samples from pl. 8—9—2, and Fig. 4 *b* from pl. 8—13. The, in the root system, mixoploid plants had normal pollen throughout after long-term treatment.

At meiosis only tetraploid PMC's have been observed in plants with large pollen and only diploid ones in plants with small pollen.

By means of submersion in 0,1 % colchicine solution for 24 hours of seedlings having about 3-mm-long coleoptiles it is thus possible to obtain adult plants in which no trace of diploidy can be discovered. In such plants meiosis may in all probability be regarded as typical of an autotetraploid *A. myosuroides*.

Complete analysis of 25 PMC's in I—M gave the following results.

Configuration	No. of PMC's
$1_{IV} + 11_{II} + 2_{I}$	1
$2_{IV} + 10_{II}$	4
$2_{IV} + 9_{II} + 2_{I}$	2
$2_{IV} + 1_{III} + 8_{II} + 1_{I}$	2
$3_{IV} + 8_{II}$	3
$3_{IV} + 1_{III} + 6_{II} + 1_{I}$	2
$4_{IV} + 6_{II}$	3
$5_{IV} + 4_{II}$	3
$5_{IV} + 1_{III} + 2_{II} + 1_{I}$	1
$6_{IV} + 2_{II}$	4

TABLE 1. *Chromosome numbers, per cent good pollen and diameter of the pollen grains in colchicine treated plants.*

(S = Submersion in 0,1 % solution for 24 hours, G = continuous germination with 0,1 % solution, 0 = untreated.)

Plant No.	Treatment	Number of plates with 2n equal to		% good pollen	Diameters of the pollen grains											Mean
		2x	4x		11	12	13	14	15	16	17	18	19	20	21	24	30	
8—9—1	S	1	24	80,5	2	5	28	40	23	2								13,8
8—9—2	S	0	25	71,0					6	13	40	43	52	40	17	1	1	18,5
8—9—3	G	13	11	93,0		2	28	39	29		1			1				14,1
8—9—4	G	11	14															
8—9—2	G	25	0															
8—13	0	—	—	73,0	1	2	18	39	31	9								14,2

From this a mean syndesis of $3{,}52_{IV} + 0{,}20_{III} + 6{,}44_{II} + 0{,}44_{I}$ per PMC is obtained. Hence only about half the number of chromosomes are associated as multivalents in this new autotetraploid. This may be

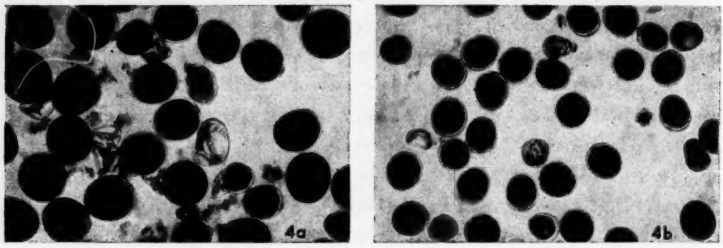


Fig. 4. Pollen grains of: *a*, a tetraploid plant; *b*, a diploid plant. × 200.

interpreted as due to the fact that the meiotic mechanism as such counteracts multivalent formation. In other words, the chromosomes function as a whole as a single pairing block in a large number of cases (JOHNSSON, 1941). The cause of this may be that the chiasmata are

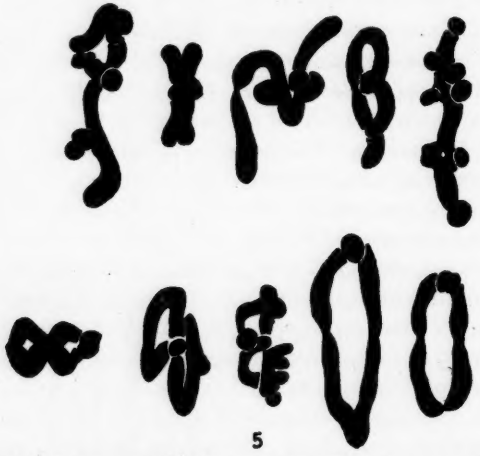


Fig. 5. Separately drawn quadrivalents of tetraploid *A. myosuroides*. × 3000.

localized to rather short proximal segments. With regard to the I—M chiasmata, which are mostly interstitial, the frequency of distal chiasmata must in any case be low. Further, any mutation of whatever kind that may occur in the future history of an autotetraploid and that lowers the quadrivalent frequency must have a positive selection value.

The very low multivalent frequency that may be found in stabilized autotetraploid species is therefore fully intelligible (JOHNSSON, 1941).

Some separately drawn quadrivalents are shown in Fig. 5. In the tetraploid condition the chiasmata are also mostly interstitial. Triple and quadruple chiasmata are exceedingly rare. The second quadrivalent in the upper row, however, has a quadruple chiasma.

VI. EFFECT OF CROSSING AND INBREEDING.

A. myosuroides, like most grasses, may *a priori* be assumed to be typically allogamous, and in connection with that shows self-sterility (incompatibility) and inbreeding depression. In *A. pratensis* F. NILSSON (1934) has found strong sterility after selfing, and in the genus *Phleum*, closely related to the *Alopecurus*, there occurs typical allogamy with self-sterility and inbreeding depression (SYLVÉN, 1929; VALLE, 1931). The cytogenetics of an allogamous plant may be studied both by crossing and inbreeding. By crossing different plants from the same or different morphological or geographical races (as in the case of the autogamous plants) the occurrence of differences in chromosome-structure with heterozygous symptoms can be investigated, and by inbreeding the presence of genic and structural differences with homozygous symptoms can be brought to light.

With these ends in view, all the original types mentioned in Chapter II were inbred and some of them crossed, the same plants being employed for both methods of pollination. The crosses were first carried out in the form of open pollination without emasculation. When the cross-pollinated panicles were ripe and harvested, all the other deflorated panicles were removed and the panicles afterwards produced were self-pollinated. This is possible when the plants continue to flower even after the earliest panicles have matured. The influence of the different modes of pollination on the seed setting is given in Table 2. The plants recorded in pairs within lines were crossed reciprocally with each other. »K» denotes crossing and »I» inbreeding. As a measure of the seed setting the percentage of spikelets bearing seed (the spikelets are one-flowered) is used. Even after cross pollination the seed yield was far from maximum, on an average only 52,7 % of the spikelets setting seed. Following selfing, however, the amount of seed set was only about half that after cross-pollination. The variation in seed production after selfing as between the plants was however considerable. Two plants even showed a somewhat better seed yield after

selfing than after cross-pollination. A test by the 0-hypothesis (FISHER, 1938) of the differences in seed setting between crossing and inbreeding gave $t = 11{,}765$, which implies that the probability of the difference being zero is $< 0{,}01$. The general conclusion that *A. myosuroides* has

TABLE 2. *Comparison between ♀-fertility after selfing and cross pollination.*

Plant	Selfing = I Cross pollination = K	Number of spikelets with seeds	Number of spikelets without seeds	Spikelets with seeds %	Germination %	Spikelets with seeds K % — I %
0—4	I	36	286	11,2	19	+ 37,8
	K	116	121	49,0	32	
Delft	K	109	69	61,2	63	+ 58,0
	I	9	270	3,2	78	
Rennes	I	403	104	79,5	43	— 1,1
	K	207	57	78,4	37	
Rouen	K	80	44	64,5	37	+ 57,9
	I	21	298	6,6	43	
Jena	I	202	289	41,1	61	+ 30,3
	K	190	76	71,4	77	
Paris	K	165	168	49,5	58	— 9,2
	I	458	322	58,7	55	
Tabor	I	30	392	7,1	83	+ 11,4
	K	37	160	18,5	54	
München	K	71	208	25,4	52	+ 22,5
	I	32	1072	2,9	56	
Nancy	I	10	650	1,5	20	+ 25,6
	K	45	121	27,1	22	
Brunn	K	129	28	82,2	13	+ 27,1
	I	353	288	55,1	1	
Mean	I	—	—	26,7	45,9	+ 26,0
	K	—	—	52,7	44,5	

inferior seed setting after selfing than after cross pollination is thus fully justified.

As is the case with other allogamous species that have been subjected to enforced selfing, the self-fertility of *A. myosuroides* is subject to considerable individual variation. A number of plants appear to possess an equally good seed production after selfing as after cross-pollination, e. g. Rennes and Paris. Others, such as Delft and Nancy,

show pronounced self-sterility. Worthy of noting is the fact that the germinability of the seed is at least as high after selfing as after cross-pollination.

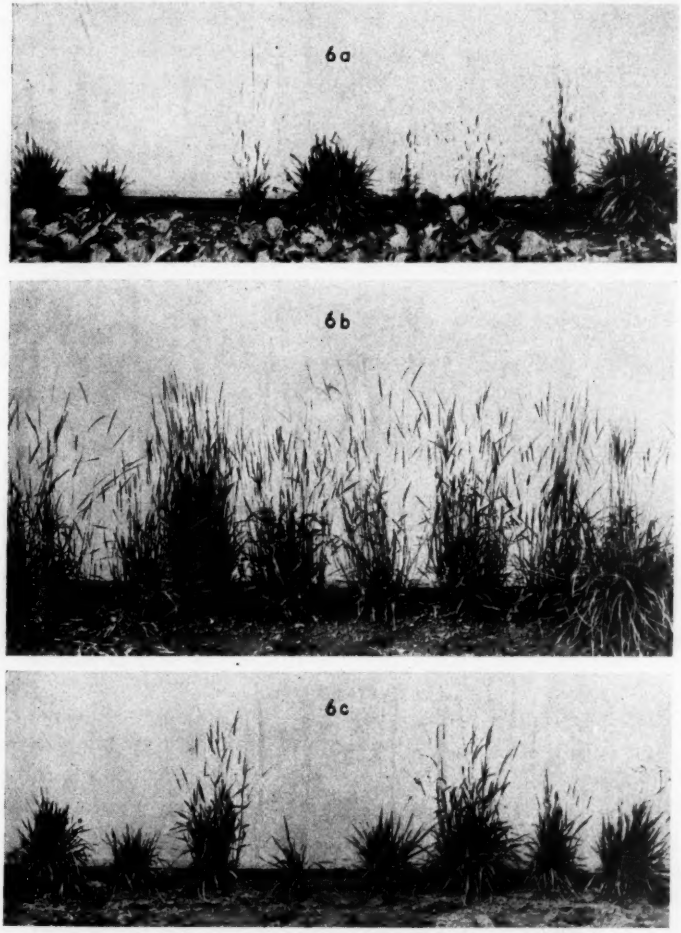


Fig. 6. Habit of inbred and outcrossed families. — Fig. 6 *a*. The I_1-progeny of Rouen (family No. 4). — Fig. 6 *b*. The F_1 family (No. 26) Rouen × Rennes. — Fig. 6 *c*. The I_1-progeny of Rennes (family No. 12).

In view of the fact that the self-sterility is far from complete the question arises whether a pure cross progeny is obtained after isolation

in pairs without emasculation. Figs. 6 and 7 illustrate two cross progenies as well as inbred progenies of the parental plants. Fig. 6 *a* gives

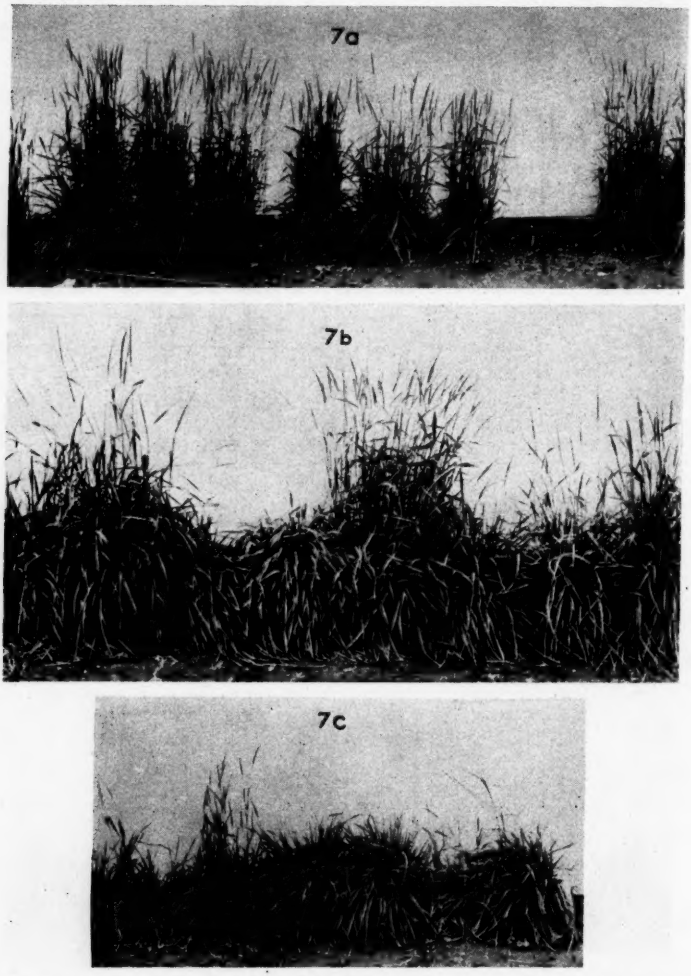


Fig. 7. Habit of inbred and outcrossed families. — Fig. 7 *a*. The I_1-progeny of Tabor (family No. 9). — Fig. 7 *b*. The F_1 family (No. 23) Tabor × München. — Fig. 7 *c*. The I_1-progeny of München.

the I_1 from Rouen, and 6 *b* the offspring of the same plant after intercrossing with Rennes 6 *c*. It will be seen that the progeny of the same

plant has entirely different habits after crossing and after inbreeding. Rouen has, however, relatively low self-fertility, 6,6 %, whereas the father plant has a high self-fertility, 79,5 %. Both the reciprocal crosses, however, agree completely in habit and therefore Rennes, in spite of its high fertility after enforced selfing, will also be — in any case almost — exclusively cross-pollinated on having access to other pollen. Figs. 7 *a*, *b* and *c* show the cross Tabor × München (7 *b*) and the I_1 progenies, 7 *a* and 7 *c*, of the parental plants. In all cases the F_1 offspring have presented different habits from that of the I_1 progenies of the parent plants, and in all cases both the reciprocal crosses have resembled each other in a high degree.

From this it is clearly seen that a pronounced selective fertilization in favour of cross-fertilization takes place when the plants have access

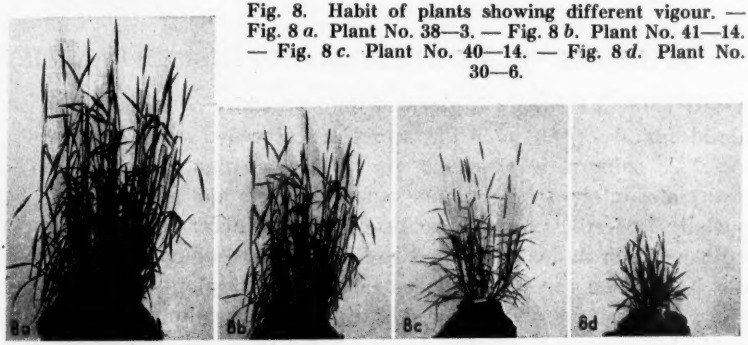


Fig. 8. Habit of plants showing different vigour. — Fig. 8 *a*. Plant No. 38—3. — Fig. 8 *b*. Plant No. 41—14. — Fig. 8 *c*. Plant No. 40—14. — Fig. 8 *d*. Plant No. 30—6.

both to their own pollen and to foreign pollen, even if the particular plant has good fertility after enforced selfing.

Figs. 6 and 7 also show the great differences that exist between different I_1 and F_1 progenies. The I_1 progenies in Figs. 6 *a* and 6 *c* show a marked depression and are almost sublethal. The I_1 progeny in Fig. 7 *a* is a rather normal, many-strawed type, while the progeny in 7 *c* exemplifies a leafy, few-strawed type. Broadly viewed, all the I_1 families can be ranged in the three categories: (1) Feeble, on the border-line of viability, (2) Normal, many-strawed, (3) Leafy, few-strawed, vigorous. After crossing, the following conditions have resulted: plant with feeble I_1 × plant with feeble I_1 → normal, many-strawed, vigorous F_1 (Fig. 6); plant with normal, many-strawed I_1 × plant with leafy, few-strawed I_1 → vigorous, leafy, few-strawed F_1 (Fig. 7); plant with leafy, few-

strawed $I_1 \times$ plant with leafy, few-strawed $I_1 \rightarrow$ very vigorous, leafy and few-strawed F_1.

Although both the I_1 and the F_1 families are a well marked mean type in habit, there is a rather essential intra-family variation, especially pronounced within the weaker families (Figs. 6 *a* and 6 *c*). Regarded as a whole the plant material shows extreme diversity in innumerable characters, such as vegetative development (Fig. 8), straw density, leafiness, leaf size, length and diameter of panicle, density of panicle, size of spikelets, colour of anther, earliness, etc. No detailed investigation, however, has been attempted of the morphological variability.

The facts set forth show that *A. myosuroides* is a typical allogamous species, with the varying self-sterility, inbreeding depression, and considerable genotypical polymorphy (especially prominent after inbreeding) characteristic of such.

VII. MALE FERTILITY IN CROSS AND INBRED FAMILIES.

In Table 3 a survey is given of the ♂-fertility of some hybrid and inbred families. As in Table 2, reciprocal crosses are given within lines. A column is provided for ♂-sterile plants, by which are meant absolutely sterile plants whose anthers do not dehisce. The partially ♂-fertile plants have been grouped according to their percentage of morphologically good pollen into classes having a class-width of 5 %. When raising progenies families of 25 plants have been the aim. On account of poor seed setting, low germinability and plant death, however, this number has been far from attained in all cases. The difference between the total number of plants and the number recorded as ♂-sterile and partially ♂-fertile is due to the fact that many plants never attained the flowering stage. In some cases these have been small and feeble plants which have either produced panicles that have not developed normally or have apparently been incapable of shooting panicles. Mostly, however, they have been vegetatively vigorous plants with weak or no straw production. Then, first of all late in the autumn as a rule single panicles have appeared which have not flowered until the advent of winter. It will be seen from Table 3 that the pollen quality of *A. myosuroides* is far from 100 % good. Only a small fraction of the different families have 95—100 % good pollen. The average good pollen for the whole material is about 80 % for both inbred and hybrid families. In this way, too, *A. myosuroides* behaves like the typical allogams, which according to MÜNTZING (1939) are characterized

TABLE 3. *The ♂-fertility in some I_1- and F_1-families.*

Mother plant	Generation	Number of plants	Number of ♂-sterile plants	Number of partially ♂-fertile plants	Percentage of good pollen														Mean
					32,5	37,5	42,5	47,5	52,5	57,5	62,5	67,5	72,5	77,5	82,5	87,5	92,5	97,5	
0—4	I_2	5		5						1	2			1				1	71,0
	F_1	9		8				1		2				2	2			1	71,9
Delft	F_1	15		12					1		3		1	1	1	1	1	3	78,2
	I_1	7		7					1	1				1		1	1	2	80,7
Rennes	I_1	25	2	14			1			1	5		4	2	1				66,7
	F_1	10		8											1		3	4	92,5
Rouen	F_1	12		11										1			7	3	91,3
	I_1	9	1	6					1	1			1			1	1	1	75,8
Jena	I_1	25		18	1		1			1		1	2	3	3		4	2	77,2
	F_1	11		4											2	1		1	86,5
Paris	F_1	11		4				1								2	1		78,3
	I_1	27		17			1					1	1	2	1	1	1	9	87,0
Tabor	I_1	25	12	12					1	2	1	2	3	1	1	1			68,4
	F_1	16	1	10					1				3		2			4	82,6
München	F_1	17		13			1	1					1	2	3	2		3	80,2
	I_1	18	2	9						1			1	1	1	1	2	2	84,6
Totals	I_1	141	17	88	1		3		3	8	8	4	12	11	7	5	9	17	77,0
	F_1	101	1	70			1	3	2	2	3		5	6	11	6	12	19	83,1

by reduced pollen fertility. When partial sterility has made its appearance in autogamous plants, it has done so in crosses between fully fertile lines such as *Pisum* (HAMMARLUND and HÅKANSSON, 1930) and *Galeopsis* (MÜNTZING, 1930). Here, however, the same sterility is found in both inbred and hybrid families. The percentage of good pollen, though, is subject to great intra- as well as inter-family variation. The variation seems to be continuous from fully fertile to strongly sterile plants. There is certainly some degree of accumulation in »semi-sterility» and »quarter-sterility», but this fact cannot be assigned significance.

A marked difference between inbred and hybrid families in the frequency of absolutely ♂-sterile plants is noticed. The inbred families show altogether 17 such individuals from four families among 141 plants, while only one ♂-sterile plant occurs among 101 hybrid plants.

VIII. CYTOLOGICAL STUDIES OF THE CROSS PROGENIES.

The greatest diminution in ♂-fertility among hybrid families is shown by Delft × 0—4 and reciprocal. This cross has therefore been submitted to a rather thorough cytological study. Thus, of the 15 plants with Delft as mother, the microsporogenesis of 14 plants has been investigated. In none of these plants, however, could any meiotic disturbance whatever be detected. A survey of the results follows:

Plant No.	% good pollen	Stages observed
1	—	—
2	60	I—M, I—A
3	79	I—M
4	95	I—M, I—A, II—M, II—A
5	95	I—M, I—A
6	62	I—M, I—A
7	54	I—M, I—A, II—M, II—A
8	—	I—M, I—A
9	—	I—M, I—A, II—M, II—A
10	70	I—M, I—A, II—M, II—A
11	98	—, —, II—M, II—A
12	61	I—M, I—A
13	86	—, —, II—M, II—A
14	93	I—M, —, II—M, II—A
15	84	I—M, —, II—M, II—A

One plant in the reciprocal cross had so low a percentage of good pollen as 49 %. In this a slight meiotic disturbance consisting in the occurrence of two univalents in approximately one PMC of 20 was observable.

The only absolutely ♂-sterile plant that occurred within the hybrid families exhibited a quite obvious univalent frequency but no other disturbances. The univalent frequency was as follows:

No. of univalents per PMC	0	2	4	6	8	10
No. of PMC's	18	32	14	5	2	1

This frequency corresponds to a mean of 2,44 univalents per PMC, counted on 72 PMC's.

Naturally enough, a partial asynapsis of this kind may be a symptom of structural hybridity, but is more probably genically conditioned (see below).

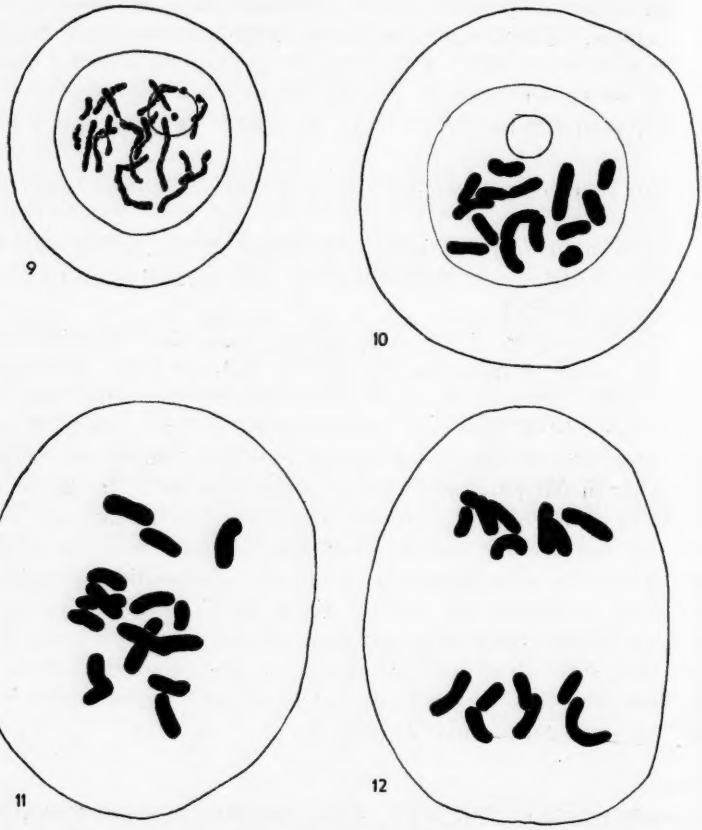
The ♂-fertility of the cytologically unexamined hybrid families does not, either, suggest that the parents had any great differences in chromosome structure. If that had been the case the plants within each F_1 family ought to have had a more uniform pollen fertility. A difference consisting, for instance, in a more extensive translocation ought to have given a fairly uniform sterility of 50 % in the F_1, as in the well-known cases of *Pisum* (E. NILSSON, 1936) and *Zea* (BRINK and COOPER, 1931) as well as other species. Similarly, a largish inversion ought to have led to the same frequency of bicentric chromatids and with it a uniformly reduced pollen fertility within the F_1 family. The number of crosses carried out is certainly small, but the conclusion seems justifiable that such structural differences as give manifest genetic and cytologic symptoms in the F_1 do not occur in *A. myosuroides*, in any case with any considerable frequency.

IX. ABNORMALITIES IN THE MICROSPOROGENESIS OF INBRED PLANTS.

Within the I_1 families and later inbred generations several distinct deviations from the normal course of microsporogenesis have appeared. These aberrations have mostly been linked up with absolute ♂-sterility. As the disturbances concerned have been of an unusual and fundamentally significant character in the majority of cases, a special description of these deviations would seem desirable.

1. ABSOLUTE ASYNAPSIS.

In an earlier work (JOHNSSON, 1941) the writer has mentioned the occurrence of genically governed absolute asynapsis in *A. myosuroides*.



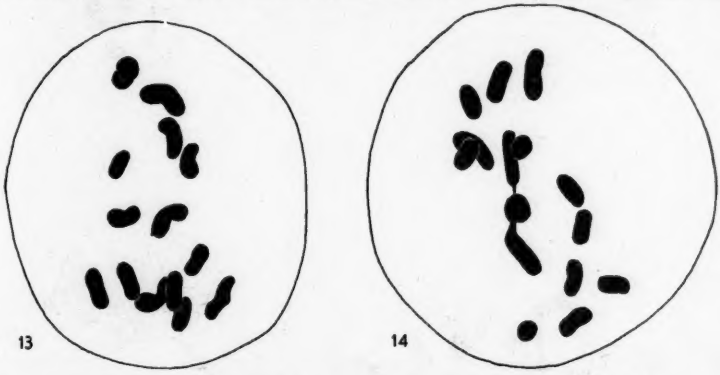
Figs. 9—12. Meiosis in asynaptic *A. myosuroides*, plant No. 35—7. — Fig. 9. Diplotene showing unpaired chromosomes. — Fig. 10. Diakinesis with 14 univalents. — Fig. 11. Stage comparable with I—M. — Fig. 12. I—A with rapid and simultaneous chromosome separation. × 3000.

Since then, this phenomenon has been observed in a rather large number of plants within various families.

As soon as the chromosomes are discernible in the later stages of prophase they have without exception, or almost so, been found to be

unpaired. Fig. 9 shows a PMC in a stage comparable with diplotene, and Fig. 10 with diakinesis. Further, in Plate I, Fig. 1, a photomicrograph is given of a diakinesis. The earlier stages of prophase have unfortunately always been too caked up to allow of any detailed observations.

No first metaphase in the strict sense occurs, although on very rare occasions chromosomes are seen to collect to some extent in the central portion of the cell, as shown in Fig. 11 and Plate I, Fig. 2. Instead, a separation nearly always occurs as soon as the nucleoplasmic surface is disintegrated. This separation proceeds in two somewhat different ways. In some plants it takes place rapidly and simultaneously, in that case

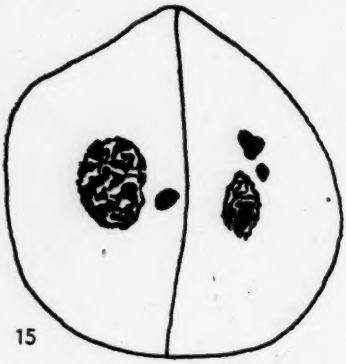


Figs. 13—14. Meiosis in asynaptic *A. myosuroides*, plant No. 35—14. — Fig. 13. I—A with slow and irregular chromosome separation. — Fig. 14. I—A with an exceptional bivalent with an abnormal chiasma. × 3000.

bringing about a very definite distribution of the chromosomes to both poles. This course of events is represented in Fig. 12 and Plate I, Fig. 3. The result will be two distinct interphase nuclei as shown in Plate I, Fig. 4. In other plants, on the other hand, the anaphase separation is more »sluggish». The chromosomes then lie a longish time spread in the cell, and their movements to the poles do not take place simultaneously, as shown in Fig. 13. The slower chromosomes then run the risk of not being incorporated in the anaphase nuclei. The consequence is that the dyad cells often contain micronuclei (Fig. 15).

In typically asynaptic plants the asyndesis is almost invariably complete. Only in extremely rare PMC's, perhaps 1 in 500, can a bivalent of abnormal constitution be found. An exceptional cell of this type is reproduced in Fig. 14.

In one plant that was asynaptic in primary type, however, a more considerable bivalent occurrence has been noted. The majority of the PMC's in this plant as well are entirely without bivalents, although



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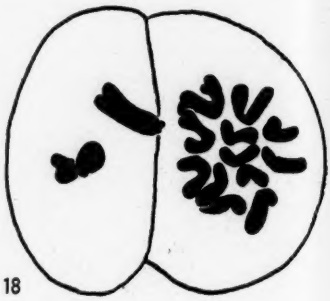

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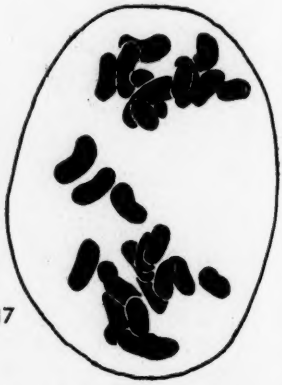

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Figs. 15—18. Meiosis in asynaptic *A. myosuroides*. — Fig. 15. Interphase with micronuclei following slow chromosome separation at I—A, plant No. 35—14. — Fig. 16. Exceptional bivalents from an asynaptic plant, No. 46—4. — Fig. 17. Syndiploid PMC with 28 univalents from an asynaptic plant, No. 46—1. — Fig. 18. II—M with unequal chromosome separation, $^{2}/_{12}$, plant No. 46—1. × 3000.

1—6 bivalents not infrequently occur. Certain portions of the loculi may show a rather high bivalent frequency, while other portions are purely asynaptic. The bivalents, however, show a non-characteristic form in that the chiasmata are almost always terminal, often filiformly drawn

out and not uncommonly incomplete (Fig. 16). Nearly all the bivalents are rod-shaped; only in a couple of cases have ring-bivalents been found.

In such PMC's as have one or more bivalents it is not unusual for one or more univalents to divide at I—A, which otherwise never occurs in the absolutely asynaptic plants.

A couple of plants have shown some frequency of tetraploid PMC's—syndiploidy. In these, too, the asyndesis has been complete (Fig. 17) and has exhibited the development characteristic of diploid PMC's.

The second meiotic division is exceedingly regular in the asynaptic plants, with normal centromere division and chromatid separation. As a consequence of the random first division there is, however, a considerable variation in chromosome number (Fig. 18), especially in plants with a »sluggish» first division. The correlation between the character of the first division and the n-number in II—M is evident from the following table:

I division	n-number in II-M												
	1	2	3	4	5	6	7	8	9	10	11	12	13
Rapid . . .	1			3	10	33	72	33	10	3			1
Slow	1	3	1	2	6	13	10	13	6	2	1	3	1

The resulting tetrads are all very regular. That the preceding meiosis had been abnormal is, however, evident from the fact that the nuclei of the young tetrads often exhibit considerable differences in size.

More or less clear cases of genically controlled asynapsis are known in several plants. A review of these has recently been published by PRAKKEN (1943). He distinguished three groups marked by different degrees of asyndesis. The third group with complete asynapsis contains, however, only a few cases, viz. *Datura stramonium* (BERGNER *et al.*, 1934), *Hevea brasiliensis* (RAMAER, 1935), *Allium amplectens* (LEVAN, 1938, 1940) and the case just described of *Alopecurus myosuroides*. To these may be added a recently described case in *Godetia Whitneyi* (HÅKANSSON, 1943). Further, in some cases of partial asyndesis, e. g. *Zea* (BEADLE, 1930), failure of conjugation is so high that complete asyndesis occurs in high frequency.

Complete asynapsis due to other causes exists in true haploids such as *Oenothera franciscana* (BRADLEY and CHANDRAKANT, 1930), *Hordeum distichum* (TOMETORP, 1939), and *Secale cereale* (LEVAN, 1942). Some species hybrids with complete asynapsis have also been described, e. g.

in *Raphanus* × *Brassica* (KARPECHENKO, 1927) and *Alopecurus utriculatus* × *A. myosuroides* (JOHNSSON, 1941). The same phenomenon also occurs in some apomicts (ROSENBERG, 1917). Further, STRAUB (1937) has found that absolute asynapsis can be produced modificatively in *Gasteria trigona* by means of powerful temperature shocks. All the cases of asynapsis mentioned here as due to different primary causes show the same meiotic course. All are examples of the *semi-heterotypical division* described by ROSENBERG (1917). A characteristic feature of this division is that the univalents are distributed at random to the two poles in I—A and divide as in normal meiosis first in II—M. This random division may proceed with great precision and result in two distinct interphase nuclei, as is most frequently the case in asynaptic *A. myosuroides*, or it may proceed slower, in which case one or more chromosomes do not reach the poles and behave as micronuclei in the interphase, as happens in certain asynaptic *Alopecurus* plants. Finally, it may be entirely suppressed, with restitution nuclei as a result, as occurs in the *Hieracium* prototype (ROSENBERG, 1917) and, with the greatest regularity, in *Allium amplectens* (LEVAN, 1940). These divergencies in behaviour are certainly only gradual and are referable to differences in the »strength» of the anaphase movements, i. e. to the spindle mechanism. DARLINGTON (1937) advanced the hypothesis that the spindle is formed through the interaction of polarized centromeres in the somatic divisions or by equivalents of these, the centromeres of the chromosome pairs in meiosis and pole centres (centrosomes). If pole centres alone can form an effective spindle, the anaphase separation in a completely asynaptic form can therefore be conceived as taking place with precision. If an effective spindle can only be formed with the co-operation of paired chromosomes, the frequency of restitution nuclei ought to be the greater the more dependent the spindle is of paired chromosomes. The fact that the spindle is normally developed in asynaptic *A. myosuroides* is shown by such views as Fig. 12. No tendency has been observed here to the extreme sinal or bent spindles that have been observed in other cases (BEADLE, 1930).

A common trait in complete asynapsis is, therefore, that the centromeres divide in the normal phase of the meiotic cycle. In partial asyndesis, on the other hand, it is usual for some or even all the univalents to divide as early as I—M. This is the case in, among others, the following genically conditioned cases of partial asynapsis: *Hordeum* (EKSTRAND, 1932), *Crepis* (RICHARDSON, 1935), *Pisum* (KOLLER, 1938), *Populus* (JOHNSSON, 1940 a) and *Secale* (PRAKKEN, 1943). The well-

known course in such cases is for the univalents to divide in a secondary metaphase plate after the bivalents have separated. Everything tends to show that the first division proceeds so quickly when only univalents are present that these have not time to divide. The occurrence of bivalents must be assumed to have a retardative effect on the development, since the state of equilibrium that I—M constitutes has a certain duration. As a result, the internal development of the univalents is able to proceed so far that these can divide. A border-line case in this respect is evidently represented by the absolutely asynaptic form of *Allium amplectens*. In this form the univalents are polarized and arrange themselves in the equatorial plane but have not time to divide before the first division is finished and restitution arises (LEVAN, 1940). In sexual organisms with absolute asynapsis centromere division seems to occur in the first division only in the classical *Pygaera* case (FEDERLEY, 1913). Here, however, there occurs the further abnormality that chromosome division takes place in the first as well as the second division. In the vegetable kingdom centromere splitting in the first division in cases of complete asynapsis seems only to be described for certain apomicts (ROSENBERG, 1917, *et al.*).

The cause of the failure of I—M pairing in genically controlled asynapsis is still unclear. In maize BEADLE (1933 a) has observed that there is normal pairing in zygotene but that the chromosomes already fall apart in early pachytene. For rye (partial asyndesis) PRAKKEN (1943) states that the pairing is approximately normal at pachytene and diplotene. In *Allium amplectens* LEVAN (1940) finds that pachytene pairing is normal but that only relational coiling holds the chromosomes together at diplotene. In *Alopecurus myosuroides* the chromosomes are unpaired at as early a point as it has been possible to make clear observations in late diplotene. BEADLE (1933 a) calculates with the following possible causes of the failure of metaphase pairing: (1) premature chromosome division, (2) non-specific pairing between non-homologous chromosomes, (3) failure of chiasma formation, (4) breakage of chiasmata, (5) deficient terminal affinity. Premature chromosome division, however, would most likely preclude pachytene pairing (the »precocity theory»), though pachytene pairing has been observed in a number of cases. That normal specific pairing should suddenly be replaced by a regular non-specific pairing sems to be very hypothetical. For *A. myosuroides* deficient terminal affinity can scarcely play any part, as normally the chiasmata are interstitial. There then remains the possibility that chiasmata are not formed, or that they

break. Breakage of chiasmata appears to be less probable, since fragments ought in that case to appear. In spite of pachytene pairing, then, the most probable cause of the asyndesis would seem to be non-formation of chiasmata. To carry this question further back is scarcely possible with our present incomplete knowledge of the mechanism of chiasma formation and chromosome reproduction.

2. PARTIAL ASYNAPSIS.

Partial asynapsis with a univalent frequency ranging, as a rule, from about ten univalents per PMC to single asynaptic chromosomes in a number of cells is a very common phenomenon within some inbred families. Evidently a varying partial asynapsis of this type also belongs to constant inbred phenomena in rye (LAMM, 1936; PRAKKEN, 1943). Genically governed partial asynapsis is, as a matter of fact, a not infrequently described phenomenon. The literature on the subject has recently been summarized by PRAKKEN (1943). To his list may be added a recently described case of Y-linked asynapsis in *Rumex acetosa* (LÖVE, 1943).

In contrast to their behaviour in absolute asynapsis the univalents not infrequently divide at I—A. Also here, however, the majority of univalents go to the poles without dividing. The behaviour of the univalents in *A. myosuroides* thus follows the *Pilosella* type as described by TÄCKHOLM (1923).

3. PREMATURE CENTROMERE DIVISION.

One of the most distinctive features of the meiotic division cycle is indisputably the locating of the single centromere division to II—M. Among sexual plants no case appears to be known of complete asyndesis in which the centromeres split in the first division. However, two sibling plants from a I_1 progeny within *A. myosuroides* have appeared in which the centromeres divide at late I—A.

Both these plants are characterized by partial asynapsis in I—M. The frequency of univalents nearly agrees in both, as indicated by the figures given below:

No. of univalents per PMC	0	2	4	6	8	10	12	14	M
No. of PMC's, Pl. 8 ..	11	27	16	2	2	0	1	12	4,59
» » » » 11 ..	17	14	3	3	1	1	0	4	3,07
Total	28	41	19	5	3	1	1	16	4,02

Apparently two different causes affect the univalent frequency: (1) one that produces fluctuating asyndesis in such frequency that two

univalents are the commonest occurrence and PMC's containing 4, 6, 8 and 10 univalents appear with ever-increasing rarity, (2) one that produces total asynapsis in the affected PMC's.

Furthermore, there are often bicentric chromatids in these plants, especially in plant 11, the majority of the PMC's here having one bi-

Figs. 19—22. Meiosis with too early centromere division, plant No. 9—8. — Fig. 19. Second prophase with all chromosomes divided. — Fig. 20. I—A with a bicentric chromosome. The chromosomes are divided. — Fig. 21. II—A with the chromosomes divided at I—A separating at random. One bicentric chromosome is present. — Fig. 22. Monad (the first division suppressed) with 3 bicentric chromosomes in II—A. × 3000.

centric chromatid in I—A or in the second division. Rather rarely, more than one bicentric chromatid is found. It should also be noted that the pollen mother-cells are unusually rounded in I—M, i. e. are in a cyto-kinetically advanced stage (Plate I, Fig. 6). These characters, partial asynapsis, bicentric chromatids, and round PMC's in I—M, are however possessed by these plants in common with many others. The

special feature of these two plants is a premature centromere division. This phenomenon is very conspicuous at second prophase, which stage invariably has the appearance given in Fig. 19. Beyond all doubt the centromeres here are divided, and the daughter-chromatids are clearly separated. The sister-chromatids often have positions quite independent of one another. Not infrequently the two dyad cells have different chromosome numbers, 14—16 (Fig. 19). This is evidently a consequence of a random distribution of univalents in I—A. Convincing evidence that the centromere division already takes place at I—A is obtained especially from PMC's with bicentric chromatids, as in Fig. 20. Instead of being, as normally, combined with a monocentric chromatid at each centromere the bicentric configuration at first division presents here the appearance of a bicentric chromatid during second division. At the same time all the other chromosomes are seen to be divided. Plate I, Fig. 5, shows a photomicrograph of late I—A in polar view, from which the centromere division that has occurred is also evident.

During division II the chromosomes are distributed at random without any metaphasic state of equilibrium occurring. In other words, all the chromosomes present the picture of lagging, split univalents. This stage has the appearance represented in Fig. 21. Although no equatorial plate is formed, one or more chromosomes are not uncommonly seen lying side by side in the equatorial plane, as in the left dyad cell in Fig. 21. This might mean (1) that centromere division fluctuates in point of time, so that occasionally a greater or less number of centromeres do not divide until II—M, (2) that divided chromosomes exert a certain amount of attraction on one another, (3) a random position.

Alternative 1 does not seem probable, as side-by-side chromosomes are rather common in II—M, while plainly undivided chromosomes have only been very seldom observed at second prophase. The third alternative, too, does not seem to provide an explanation, seeing that the phenomenon gives the impression of significance. Hence alternative 2, implying a certain attraction between chromosomes, seems to be the most likely one. Nor does this explanation seem so unreasonable in the light of the facts known concerning secondary pairing. As is also otherwise the case when bicentric chromatids occur, the dyad wall also here often cuts through the chromatid bridge as indicated in Fig. 21. Fig. 22 shows a monad with three bicentric chromatids of the second division. Probably the occurrence of these three I—A bridges has counteracted wall formation.

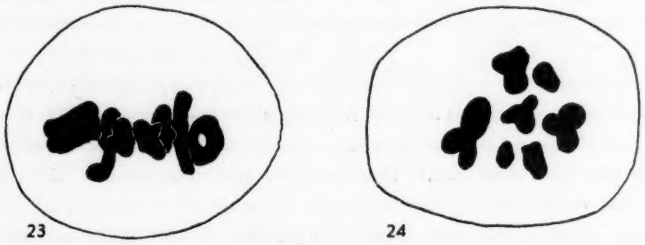
The tetrads of these plants are otherwise all 4-celled, although micronuclei occur in abundance.

This precocity of the centromeres can be put into association with the unusually spherical shape of the pollen mother-cells, which undoubtedly indicates that cytokinesis is abnormally advanced in relation to the chromosome cycle. The first division may be conceived as having proceeded uncommonly slowly, so that the centromeres have already had time to get ready for division at I—A. In other cases of retarded first division, however, this result has not been attained (see below). From this it seems assumable that the centromere division as such is premature. Thus, the centromere division itself would seem to be subject to a genotypical variation. Cases of a more accelerated centromere division, in which this already occurs at I—M, are quite feasible. Such a case in combination with absolute asyndesis should lead to the so-called mitotisized meiosis which characterizes certain apomicts (ROSENBERG's *pseudoillyricum* type) and to the »pseudo-homotypic» metaphase (GUSTAFSSON, 1935). This course of division might thus be brought about by the concurrence of genic (genotypic) asynapsis and centromere precocity, and not be a mechanical consequence of retarded meiosis as DARLINGTON contends (1937). This latter conception has also been contested by GUSTAFSSON (1935) among others.

4. ABNORMAL CONTRACTION.

A. CHIEFLY LIMITED TO I—M.

The progenies after self-fertilization, I_1 as well as later generations, from the two sources, Rennes and Rouen, as well as the products of



Figs. 23—24. Abnormal contraction in I—M, plant No. 4—1. — Fig. 23. I—M in side view. — Fig. 24. I—M in polar view. × 3000.

intercrossing between these plants, uniformly possess an abnormal chromosome contraction in I—M. These abnormal I—M chromosomes

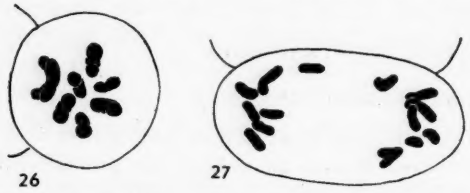
are illustrated in Fig. 23 (side view) and Fig. 24 (polar view). The same cells are photographed in Plate II, Figs. 3 and 4. For comparison with the normal bivalent morphology reference may be made to Fig. 3 (p. 473). It may be to some extent incorrect to denote these chromosomes as abnormally contracted. Their appearance suggests rather the picture of an abnormal swelling. Apparently, moreover, the chiasm-

25

Fig. 25. The separately drawn chromosomes ($6_{IV} + 1_{III} + 1_I$) from a PMC from the tetraploid plant, No. 48—7 c, with abnormal contraction. × 3000.

ata are not terminalized much more than normally, although they are often levelled out through the »swellings». The majority of the plants with this abnormality are in other respect quite regular. Syndesis is perfect, and meiosis proceeds to regular tetrads without disturbances.

After seed from one of these families had been colchicine treated by the method given above, plants were obtained in which exclusively tetraploid root-meristem cells and pollen mother-cells were observed. In these plants as well there was a typical abnormal chromosome contraction at I—M. Separately drawn chromosomes from a PMC with $6_{IV} + 1_{III} + + 1_I$ are shown in Fig. 25. The normal multivalent appearance is given in Fig. 5 (p. 476). Here, the chiasmata give the impression of being more terminalized than in the diploid plants. The syndesis is approximately the same as in normal tetraploids.



26 27

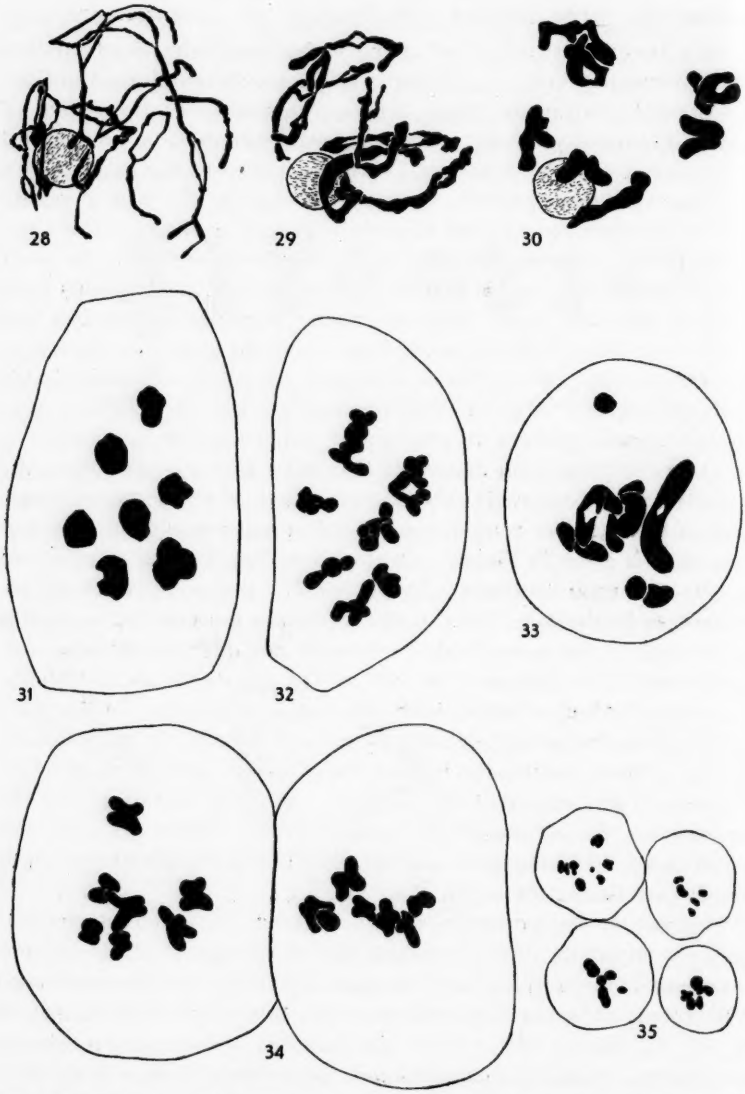
Figs. 26—27. Abnormal contraction in the second division, plant No. 12—25. — Fig. 26. II—M in polar view. — Fig. 27. II—A in side view. × 3000.

This abnormal contraction is confined to I—M in most of the plants. In a few plants, however, an abnormally strong contraction has also been found in division II, without any other disturbances having been observed. The appearance of the second metaphase in polar view in such cases is shown in Fig. 26, while Fig. 27 shows II—A.

B. COMBINED WITH MARKED RETARDATION OF MICROSPOROGENESIS.

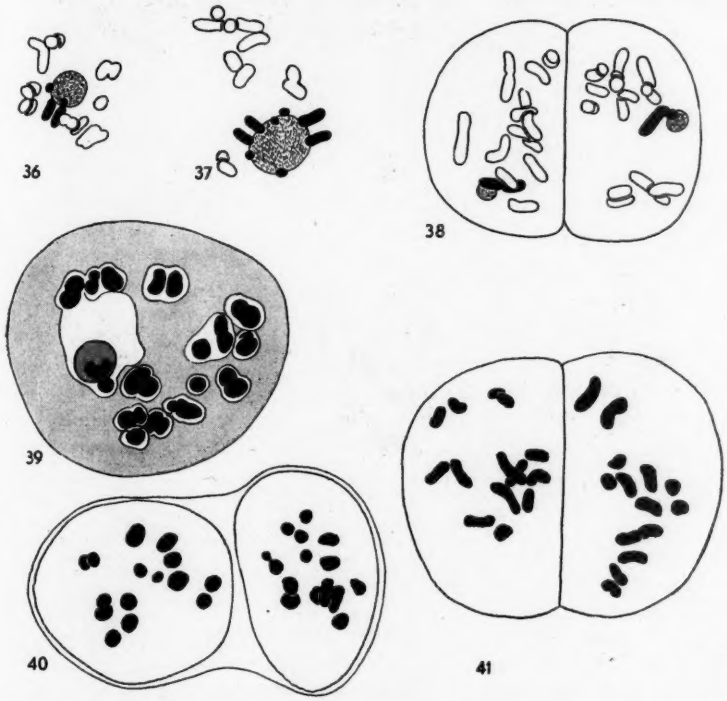
In a few plants, partly belonging to previously-described families with hypercontraction in I—M, partly belonging to families with otherwise normal contraction, there occurs, extended over the whole of meiosis, abnormally strong contraction combined with a pronounced retardation of microsporogenesis. Different plants of this type display somewhat varying behaviour, especially as regards the final breaking off of microsporogenesis and the occurrence of abortion. The chief feature of the process, however, is on the whole uniform. In I—M there is always an extremely strong contraction and the bivalents have an almost spherical form. Different stages of contraction during first division in a plant with unusually clear prophase stages are shown in Figs. 28—31. Fig. 28 no doubt represents pachytene. The pairing is clearly incomplete. Diplotene is illustrated by Fig. 29. Already here the chromosomes present an abnormally swollen appearance, which is still more conspicuous in diakinesis (Fig. 30). Seen in polar view the bivalents in I—M resemble structureless lumps of chromatin, as illustrated in Fig. 31. For comparison a I—M in polar view from a normal sister plant is given in Fig. 32. In side view, Fig. 33, it is clearly seen that the abnormal contraction here stands in clear relation to an abnormal terminalization. Most of the chiasmata are terminal or nearly so. A more or less considerable asynapsis not infrequently occurs in these plants. For instance, the cell in Fig. 33 shows six univalents. In some plants the second division may go on to tetrads. In that case there is always an extremely strong contraction in II—M, as shown in Fig. 34. When tetrads are formed these mostly present the picture of a more or less advanced degeneration. A typical feature is that the chromosomes do not despiralize and that new nuclei are thus not reconstructed. The chromosomes remain individually discernible until the cells are finally destroyed (Fig. 35).

A plant whose sporogenesis often continues to tetrads is characterized by unusually distinct nucleoli during interphase. Here a very convincing connection between the nucleolus and a chromosome could be observed. A typical II-prophase from this plant is illustrated in Fig. 36. In solitary PMC's there was, however, an uncommonly large nucleolus, to which two chromosomes were attached (Fig. 37). The explanation of this is obviously to be sought in the fact that the plant in question was partially asynaptic, having an average of 0,56 univalents per PMC. Probably the two nucleolated chromosomes (satellite chromosomes) had sometimes been unpaired and both of them had



Figs. 28—35. Abnormal contraction and retarded microsporogenesis, plant No. 10—13; Fig. 32, plant No. 10—12. — Fig. 28. Pachytene. — Fig. 29. Diplotene. — Fig. 30. Diakinesis. — Fig. 31. I—M in polar view. — Fig. 32. Normal I—M in polar view from a sister plant. — Fig. 33. I—M in side view showing exceptionally terminalized chiasmata. — Fig. 34. II—M showing abnormal contraction but otherwise normal behaviour. — Fig. 35. Degenerating tetrad with as yet visible chromosomes. × 3000.

then at times been drawn into the same interphase nucleus. As will be seen in Figs. 36 and 37, the chromatids of the nucleolus-carrying chromosomes have drawn apart. Probably, however, the centromere is undivided in them, too. Chromatid separation in II—A is often irregular; both the chromatids of some chromosomes may be incorporated



Figs. 36—41. Abnormal contraction and retarded microsporogenesis. — Fig. 36. II-prophase with one chromosome attached to the nucleolus. The chromatids are drawn apart. — Fig. 37. II-prophase with two chromosomes attached to the nucleolus. Presumably both satellite chromosomes have been included in the same interphase nucleus. — Fig. 38. II—A showing irregular chromosome separation and early reconstruction of the nucleolus. (Figs. 36—38 plant No. 9—16.) — Fig. 39. PMC with meiosis retarded in I—A, plant No. 12—5. — Fig. 40. More advanced stage with meiosis retarded in second prophase. — Fig. 41. Retarded second prophase. The chromosomes are presumably divided. (Figs. 40—41, plant No. 36—5.) × 3000.

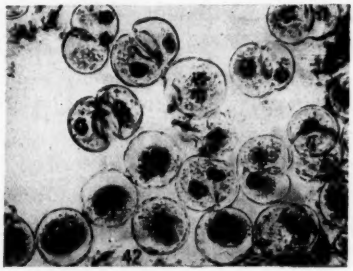
with the same telophase nucleolus (Fig. 38). This figure also shows an abnormally early re-construction of the nucleoli.

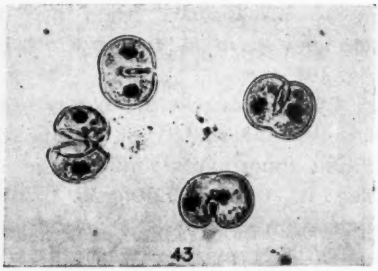
In the majority of plants marked by retarded meiosis, however, microsporogenesis never proceeds so far as to tetrads in many pollen mother-cells. Development may already cease definitively after I—M. In such pollen mother-cells the chromosome movements cease during I—A. The result will be a monad with the 14 chromosomes scattered in the cell, as indicated in Fig. 39. In such a cell every individual chromosome may be surrounded by a more refractive layer of plasm and thus constitute a micronucleus, or else several chromosomes may enter into the same micronucleus. A nucleolus is developed only in one micronucleus. The chromosomes never despiralize, but the centromeres seem to divide, at any rate in some chromosomes. The cell remains for a long time in this state, during which there is some thickening of the wall. In loculi that partly contain tetrads or uninucleate pollen-grains numerous pollen-like cells with 14 partially divided chromosomes scattered in their lumina are therefore encountered. A photograph of a cell of this type is given in Plate II, Fig. 7.

The most usual course of events is, however, that first anaphase is completed and that despiralization takes place after this, but that the meiotic cycle thereafter stagnates in the prophase of division II. A typical dyad has then developed. As a rule, there are seven chromosomes in every dyad cell. In plants with partial asynapsis one or two chromosomes too many or too few may occur. The chromosomes are much contracted, their chromatids are parallel but at some distance from each other (Fig. 41). The distance between the sister-chromatids is approximately equal to the breadth of the chromatids. Whether the centromeres are really divided or are greatly attenuated has not admitted of being decided with certainty. Probably they are divided, however. Photomicrographs illustrating this phenomenon are given as Figs. 1 and 2 in Plate II. The photographs were taken on squeeze preparation in aceto-carmine. Fig. 2 shows pollen mother-cells with ± normal second divisions and tetrads, Fig. 1 cells of the same age from the same plant with meiosis stopped in second prophase. The only further development is that the chromosomes are condensed still more, at the same time as the cell-wall is thickened and the cell assumes an appearance more like a pollen-grain (Fig. 40 and Plate II, Fig. 8). More rarely the development stops in a more advanced second division, the result then being a stage comparable with normal uninucleate pollen as shown in Plate II, Fig. 5.

In one plant presenting this cytological behaviour cytokinesis

continued further than usual and led to »pollen-grains» with normal exine. A photograph of squeezed aceto-carmine preparation from this plant is given in Fig. 42. Here, among other things, apparently uninucleate, normally round grains occur. In reality the »nucleus» in these grains consists of 14 individual chromosomes with two chromatids, and is the result of a meiosis that has stopped at I—A as indicated in Fig. 39. Other spherical, one-celled grains have two closely adjacent chromosome groups with seven double chromatids in each. In such cases meiosis has stopped in later I—A. In other cells the two second-prophase groups lie further from each other, and are then often separated by an incomplete wall. This incomplete wall formation is further illustrated in Fig. 43.





Figs. 42—43. Photomicrographs of pollen grains from a plant, No. 36—5, with retarded meiosis. — Fig. 42. The nucleus in the uninucleated grains is built up of 14 chromosomes with two chromatids; meiosis has been retarded in I—A. The nuclei in the binucleated grains are each composed of 7 chromosomes with two chromatids; meiosis has been retarded in second prophase. — Fig. 43. An imperfect cell wall is sometimes formed between the nuclei. × 300.

Different plants exhibit dissimilarities in various details, above all, in the developmental stage of the pollen mother-cells at the final cessation of meiosis, but even one and the same plant may show rather great differences between the pollen mother-cells, especially with regard to the stage of the cell when development ceases. Without doubt, in all these plants, one and the same disturbance in microsporogenesis is concerned. The phenomenon is undoubtedly well characterized by the term *retarded meiosis*. The problem is: what is it that is actually retarded? Probably the primary cause is not to be sought in the disturbance of the internal development of the chromosomes. These divide at pachytene (or at some other stage), they spiralize and go on doing so to an unusually high degree, at I—M apparently under

simultaneous increase of »matrix substance» (nucleic-acid deposit; ELVERS, 1943). The centromeres also seem to be able to divide. There is, however, a marked abnormality in the chromosome cycle, as despiralization in II division does not take place.

In all probability the basic cause lies in imperfections of the spindle mechanism. Retarded development of the spindle in division I leads to, firstly, a retarded orientation of the chromosomes in the metaphase plate, secondly, an unusually long metaphase stage. During these protracted stages spiralization proceeds at the same time as the matricial substance is increased. Occasionally an effective spindle is never formed during the first division, but the cells remain in the state shown in Fig. 39. An especially common phenomenon is a more or less ineffective spindle mechanism in division II: no metaphase develops, but the chromosomes retain their prophase orientation while spiralization goes on, in addition to which centromere division probably occurs (Fig. 40).

Cytokinesis may proceed rather normally with differentiation of a normal pollen wall (Figs. 42 and 43).

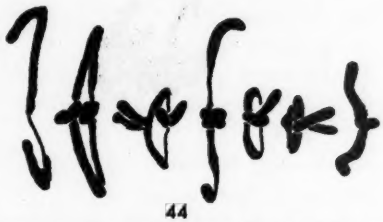
An abnormality similar in several respects has been described by FABERGÉ (1937) in *Lathyrus*. This author considers that the ultimate suppression of meiosis is caused by an alteration in the colloidal properties of the plasm in *Lathyrus*. This may amount to the same thing as failure of spindle or an ineffective spindle, for the spindle is to be regarded as caused by an orientation of the plasm molecules (DARLINGTON, 1937) and must thus depend on the colloidal constitution of the plasm. In *Lathyrus*, too, there is a markedly abnormal chromosome contraction in combination with retarded development. Parallel with the increased spiralization there also appears a very distinct increase in terminalization. The same also applies to at least some *Alopecurus* plants.

A similar instance of retarded meiosis has also been described in *Zea* (CLARK, 1938). Here, meiosis stops in I—A, and interphases then arise with several nuclei containing one to several chromosomes (cf. Fig. 39). A phenomenon to some extent resembling this has been described also in *Zea* by BEADLE (1932 a). The chief feature in this case is failure of wall formation after first division, fusion of the spindles in second anaphase, and an end-result of 40 chromosomes distributed in the cell, which are organized in micronuclei.

Defective wall formation resulting in pollen similar to that shown in Fig. 43 has been found in *Leontodon hispidus* (BERGMAN, 1935) and

Zea (LEBEDEFF, 1940). In these species, however, meiosis has been regular.

Genotypically controlled differences in chromosome size during the first meiotic division were first described by LESLEY and FROST (1927) in *Matthiola incana*. In this case, though, the state of abnormal contraction was represented by the extremely long, unusually weakly spiralized chromosomes.



44

Fig. 44. The separately drawn bivalents of one PMC from plant No. 44—18 showing an exceptionally low degree of spiralization. × 3000.

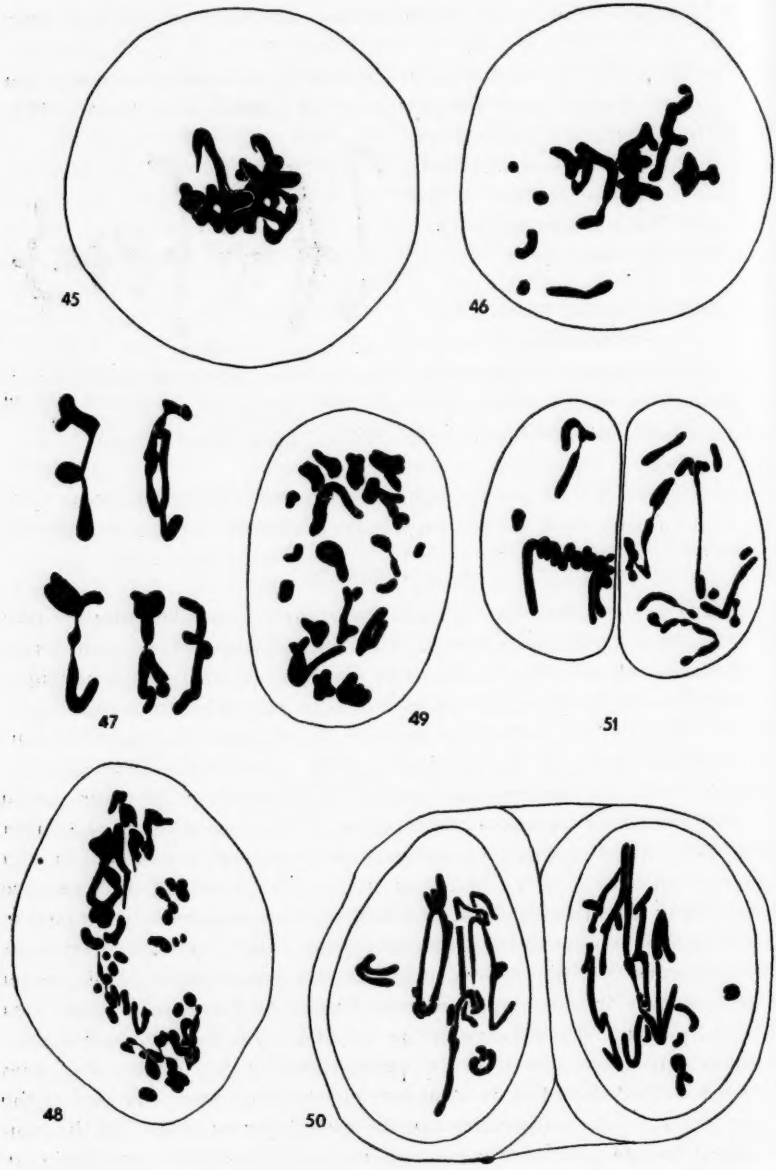
5. ABNORMALLY WEAK CONTRACTION.

The opposite of hypercontraction, abnormally weak contraction in I—M, was found in a single plant. Separately drawn bivalents from a PMC are illustrated in Fig. 44. Unusually weak contraction of this kind occurs especially in inbred rye (LAMM, 1936).

6. STICKINESS.

In *Zea mays* BEADLE (1932 b) has found a peculiar abnormality and has described this as stickiness. Within some inbred families of *Alopecurus myosuroides* there often occur ♂-sterile plants having a meiosis that is in high agreement with this stickiness in maize.

In most of the sticky plants the I—M plate is simply a conglomeration or mass of chromatin, within which the individual chromosomes are not distinguishable (Fig. 45). At times, however, single I—M plates may be more differentiated. Such a plate is shown in Fig. 46. Paired chromosomes as well as fragments are then seen. In the reproduced cell seven bivalents and five fragments of different size are clearly discernible. Some bivalents are undoubtedly asymmetric, such as the two furthest to the left in the figure. Fig. 47 illustrates some further peculiar »bivalents» (drawn separately). The second configuration in the upper row probably contains more than two chromosomes. The chiasmata are so abnormal that a clear understanding of the structure of the configuration is impossible. Nor does it seem excluded that more than two chromosomes are included in the first and second configurations in the lower row as well. All the configurations are asymmetric, with abnormal chiasmata, some distinctly incomplete.


45
46
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50

The first anaphase usually gives a very bizarre impression. Its most marked features are extremely great fragmentation and chromatin threads that bind the polar collections of chromatin. A I—A of this type is seen in Fig. 48. Not a single chromosome of unaltered, normal structure can be detected here. In solitary PMC's the alterations may be somewhat less radical, as in Fig. 49. Here it seems possible that a few chromosomes may be unaltered. Even here, however, the aberration is so great that no clear conception can be gathered of the nature of the changes.

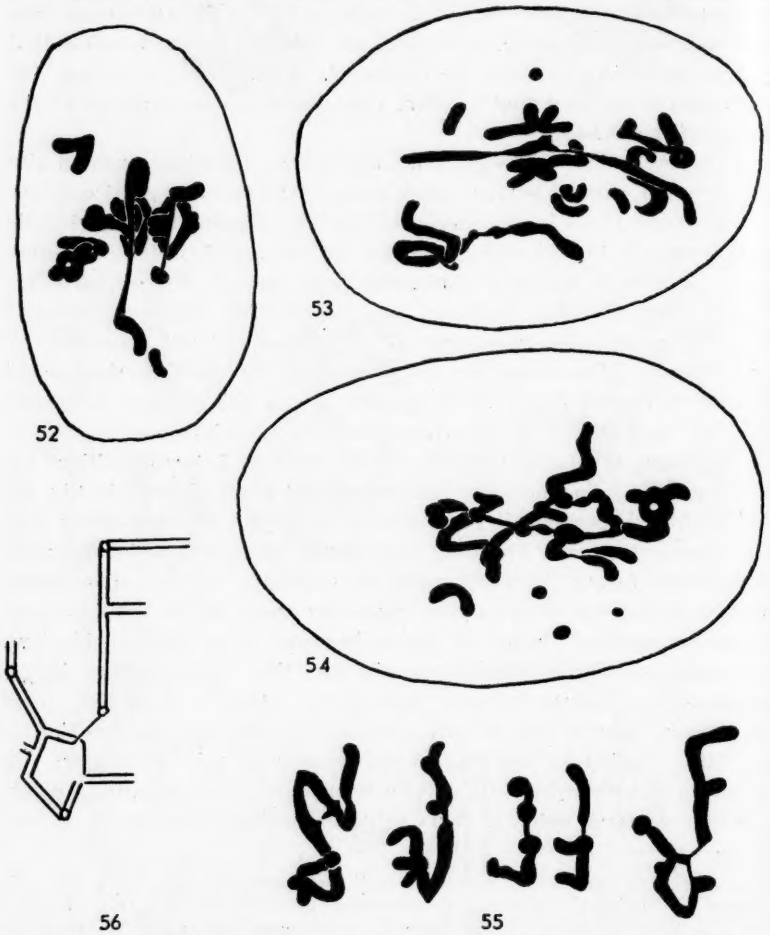
The interphase is always characterized by nuclei of unequal size and irregular outline, besides which micronuclei occur in great number.

A typical II—A is reproduced in Fig. 50. Especially characteristic of this stage is the invariable presence of chromatid bridges. It often seems as if only bicentric chromatids and acentric fragments occur. Furthermore, it often appears as though the different bicentric chromatids are not independent of each other but are connected by anastomoses. The anaphase cell in the figure showing the second division in Fig. 51 is somewhat clearer. From this figure it is clearly seen that new and peculiar chromosome structures have developed.

A couple of plants, however, offered slightly better conditions for interpretation. An unusually »normal» I—M is represented in Fig. 52. The definite impression is given that six bivalents, two univalents, and one fragment occur. The long, rod-shaped bivalent has, however, an exceptional form. A considerable accentuation of the abnormality appears in Fig. 53. Five smaller fragments occur and in addition seven larger formations. None of them, however, is a normal bivalent. Especially worthy of attention is the fact that several of the longer chromosomes appear in some way to be »slack». Still, they must necessarily possess one or two centromeres, although the position of the latter cannot be determined on account of this »slackness». It seems, in other words, as though the centromeres have wholly or partly lost their dynamic activity. Very often, exceedingly complex I—M con-

Figs. 45—51. Meiosis in *A. myosuroides* with sticky chromosomes. — Fig. 45. I—M without distinguishable individual chromosomes, plant No. 18—6. — Fig. 46. I—M with $7_{II} + 5$ ff. Several of the bivalents are asymmetrical, plant No. 40—6. — Fig. 47. I—M configurations, separately drawn, with two or more chromosomes and abnormal chiasmata, plant No. 40—3. — Fig. 48. Typical I—A showing abundant fragmentation, plant No. 18—6. — Fig. 49. I—A with less pronounced fragmentation, plant No. 44—14. — Fig. 50. Typical II—A with several chromosome strings and fragments, plant No. 18—6. — Fig. 51. Somewhat more distinct II—A showing new types of chromosomes, plant No. 40—13. × 3000.

figurations occurred. One such is illustrated in Fig. 54. Here, all or in any case most of the chromosomes look as if they were joined together into a single peculiar »multivalent». The anastomoses have not, however, the character of normal chiasmata. No congression of



Figs. 52—56. I—M in plants with sticky chromosomes. Fig. 52, plant No. 44—14; Figs. 53—56, plant No. 44—9. — Fig. 52. I—M certainly with $6_{II} + 2_{I} + 1$ f. — Fig. 53. I—M showing 7 larger configurations of abnormal shape and 5 fragments. — Fig. 54. I—M with most of the chromosomes united in one configuration. — Fig. 55. Some I—M configurations drawn separately. — Fig. 56. Diagrammatic interpretation of the right configuration in Fig. 55. × 3000.

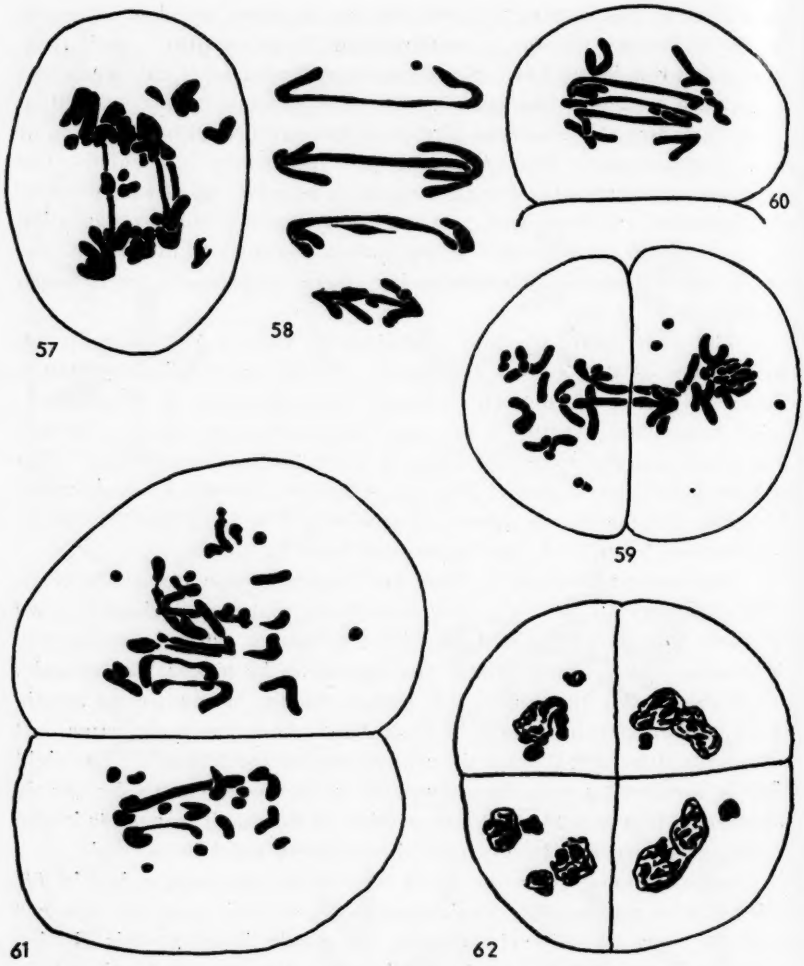
the centromeres occurs in consequence of their deficient dynamic activity. Besides this large configuration, there are three small fragments and one larger one. Some less complicated I—M configurations are drawn separately in Fig. 55. Three of them undoubtedly contain more than two chromosomes, the other two are probably composed of two chromosomes. The chiasmata are everywhere abnormal. The configuration furthest to the right seems to be made up of four more or less complete chromosomes. An attempt to analyse this configuration has been made in Fig. 56. When such a multivalent dissociates, the result must under all conditions be several structurally re-arranged chromatids.

The first anaphase may occasionally possess as »normal» an appearance as that shown in Fig. 57. At the upper pole are plainly collected four ± normal chromosomes and the arms of three bicentric chromatids. At the lower pole there are only three ± normal chromosomes, the fourth seeming to have become fragmented. The bicentric chromatids give an impression normal for such. Some further bicentric chromatids are drawn separately in Fig. 58. The three lower are derived from I—A, the uppermost from II—A.

The second division in these two plants is also unusually clear. Fig. 59 shows II—M. The two metaphase plates are joined by two bicentric chromatids, which also here present a normal appearance. The monocentric chromosomes also appear to be normal in the main. Their chromatids, though, seem in certain cases to be of different length. The number of centromeres in each dyad cell is about the same. At all events there are at least six centromeres in the left cell. The right one is so crowded that the number of centromeres cannot be clearly observed. It is possible that one or other of the small fragments is also centromere-carrying, in any case the majority must be acentric.

In exceptional cases the II—A may be as clear-cut as in Fig. 60, where three monocentric chromosomes lie at each pole and the cell contains three bicentric chromatids. As a rule, however, this division presents the appearance given in Fig. 61. The amount of chromatin is often different in the two daughter-cells. Hardly any chromosome with normal structure occurs; instead, there are numerous fragments of various sizes, bicentric chromatids, and chromatids that exhibit signs of violent structural re-arrangement.

The tetrads are all quadrinucleate but differ sharply from normal tetrads by their unequal nuclei, which, moreover, are irregularly lobulated. Micronuclei are common (Fig. 62).



Figs. 57—62. Meiosis in plants with sticky chromosomes. — Fig. 57. I—A with three chromosome bridges and fragments, plant No. 44—14. — Fig. 58. Chromosome bridges drawn separately, plant No. 44—14. — Fig. 59. II—M with two bicentric chromosomes connecting the dyad cells and several fragments, plant No. 44—14. — Fig. 60. Unusually clear II—A with three bridges, plant No. 44—14. — Fig. 61. Typical II—A showing many fragments, bicentric chromosomes and other structurally re-arranged chromosomes, plant No. 48—16. — Fig. 62. Tetrad showing irregularly lobed nuclei and micronuclei, plant No. 44—9. × 3000.

With a single exception all the preparations from sticky plants have only contained PMC's with typically sticky meiosis. In the exception meiosis was normal at a number of loculi while other meioses in the same floret were markedly sticky.

A summary of the phenomena which characterize this stickiness follows.

(1) I—M often shows a single chromatin mass without distinguishable individual chromosomes.

(2) The chiasmata have an abnormal form.

(3) Abnormal and often very complicated multivalents are common.

(4) Numerous fragments already appear in I—M.

(5) The dynamic activity of the centromeres appears to be reduced in I—M.

(6) At I—A numerous fragments and bicentric chromatids appear.

(7) At II—A fragments occur in great number as well as bicentric and structurally altered chromatids. Frequently, normal unaltered chromatids are not found at all.

This description agrees almost point for point with BEADLE's description of the corresponding phenomenon in maize. In sticky maize plants there were also anomalies in the somatic divisions. Thus, in the root meristem 9 % of the divisions were aberrant, with deviations in the form of monosomy, trisomy, fragments, deficiencies, fusions, and ring chromosomes. Unfortunately, no examination has been undertaken of the somatic divisions in *Alopecurus*. BEADLE (1937) states that these sticky plants resemble plants that have been exposed to strong X-irradiation. The resemblance is, indeed, very striking. Thus, MATHER (1934) finds that X-irradiation of the meiotic prophase in *Vicia* and *Tradescantia* causes multiple configurations and considerable fragmentation. Bicentric chromatids appear in I—A. The same is the case in II—A, where structurally altered chromosomes, ring chromosomes, etc. also occur. LEVAN (1937) has made much the same observation in *Allium Schoenoprasum*. Here, too, there are associations of several chromosomes in I—M. Especially characteristic, however, is the extreme fragmentation and the numerous chromatid bridges in I—A and II—A. Further, in the pollen mitosis all kinds of anomalous chromosome types have been observed.

In a recently published paper ÖSTERGREN (1944) has announced that ethylene glycol produces typical sticky symptoms in root mitosis

of *Allium Cepa*. Unfortunately, the direct influence of this substance on meiosis has not been investigated.

These three causes, genotypic control, X-irradiation, and treatment with ethylene glycol, thus seem capable of producing the same effect, of which stickiness is to be regarded as a symptom. In all probability the chromosome changes are secondary and the primary effect something else. DARLINGTON (1942) assumes that the cause of stickiness is to be sought in a disturbed nucleic-acid metabolism in the chromosomes. However, with our present very deficient knowledge of the physical as well as the chemical processes that are at work during the prophase stages of meiosis, we have practically no criteria by which to judge this hypothesis.

A particularly interesting question is whether the chromosome alterations associated with stickiness are of the same nature as structural changes in general. Respecting X-ray induced stickiness in *Allium*, LEVAN (1937) pronounces the opinion that here no doubt it is often simply a question of »Verklebungen» between chromosomes, in which case mechanical ruptures must follow. A similar impression is sometimes also received in cases of genotypical stickiness in *Alopecurus*.

No doubt, however, reasons can be adduced in corroboration of the view that at bottom stickiness is the same phenomenon as structural changes in general. In any case X-irradiation of moderate strength has been followed generation after generation by permanent structural changes (e. g. GOODSPEED and AVERY, 1930). Further, BEADLE (1937) has found that permanent structural alterations occur in sticky maize. Maize plants with stickiness are certainly highly sterile, but solitary seeds can be obtained after crossing sticky forms with normal plants. Among altogether 829 such F_1 plants BEADLE found 20 partially sterile ones. Of these, 13 showed a quadrivalent, thus revealing translocations. A considerable frequency of »gene» mutations (endosperm and chlorophyll characters) was also discovered. It would thus seem that in sticky plants any chromosomes and structural re-arrangements that enter gametes, the constitution of which is vital, can survive during succeeding generations in the same way as other changes, whether spontaneous or induced. It therefore appears probable that the structural changes which occur during meiosis in genotypically sticky plants are essentially of the same nature as other structural changes. Sticky plants differ in this respect from normal plants only in the immensely increased frequency with which for some unknown reason structural changes occur.

7. POLYMITOSIS.

In four sibling plants an abnormality has appeared that resembles to a great extent the polymitosis in maize described by BEADLE (1931).

Meiosis is on the whole normal in these plants. A slight asyndesis occurs, however, as is to be seen from the following table:

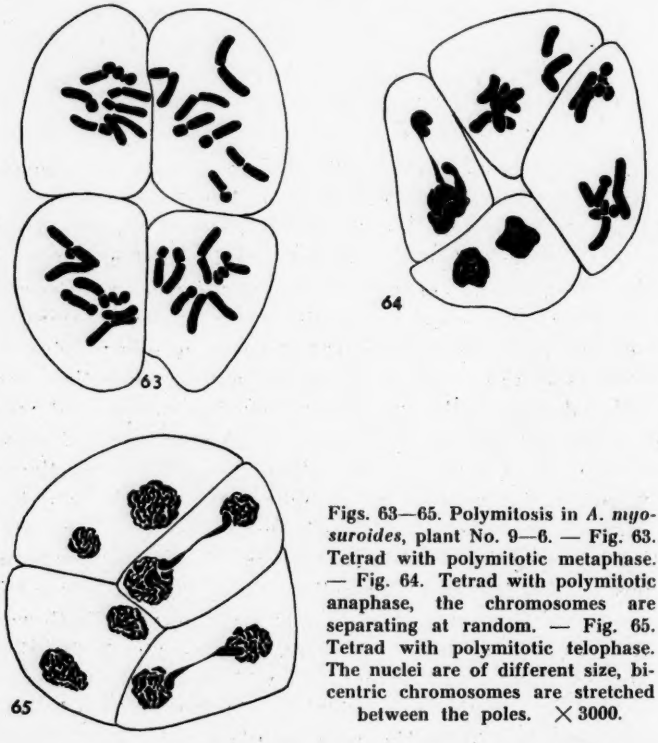
	No. of univalents per PMC				
Plant No.	0	2	4	6	M
6	44	14	2		0,60
7	81	63	15	1	1,20
15	67	13			0,33

In addition, bicentric chromatids and fragments occur in plant 6 and plant 7; in plant 6 commonly and in plant 7 rarely.

Behaviour of an unusual kind has, however, been observed immediately after the end of the second meiotic division. After an exceedingly short resting stage the tetrad nuclei enter prophase again. The individual chromosomes are observable as loose »spirals», not unlike chromosomes during the first stage of meiotic prophase. The chromosomes contract rapidly, however, and arrange themselves in the equatorial plane of the tetrad cells. There then appear the pictures reproduced in Fig. 63 and Plate II, Fig. 6. A very beautiful metaphase is thus formed, with spindles at right angles to those of the second division, and therefore the four metaphase plates of the tetrad are almost always seen in polar view. The metaphase stage appears to be of rather long duration; in any case this stage is often contemporaneous in almost all the tetrads of an anther. The centromere constrictions are very clear and confirm the somatic idiogram with its three larger chromosomes with median centromere, three smaller with submedian centromere and one small chromosome with median centromere. This is clearly seen from the upper right cell in Fig. 63, in which all the chromosomes are extended in the same plane.

The following anaphase has the character of a random distribution of the seven chromosomes to both poles (Fig. 64). Thus, the chromosomes do not undergo longitudinal division. Most frequently they show a 4—3 distribution, but all possibilities are realized. Not infrequently, for instance, cells are found in which only one or two chromosomes lie at one of the poles. The anaphases often occur at different times within cells of the same tetrad, as indicated in Fig. 64. As will be seen from Fig. 65, the chromosomes despiralize in a normal way after com-

pletion of the division, and new nuclei are reconstructed. The same picture also shows the presence of chromosome bridges in this anaphase. Such bridges were especially common in plant 6, which also often had bicentric chromatids during meiosis. In all probability the chromosome bridges appearing in polymitosis are bicentric chromatids from meiosis. As many bicentric chromosomes as are extended between the



Figs. 63—65. Polymitosis in *A. myosuroides*, plant No. 9—6. — Fig. 63. Tetrad with polymitotic metaphase. — Fig. 64. Tetrad with polymitotic anaphase, the chromosomes are separating at random. — Fig. 65. Tetrad with polymitotic telophase. The nuclei are of different size, bicentric chromosomes are stretched between the poles. × 3000.

poles in II—A must be assumed to pass with both their centromeres to one or the other of the poles. Of these, half ought to behave as bridges in a polymitotic division (as in pollen mitosis). The result of this divison will be octads. Mostly, of course, these nuclei lie in different planes, but one or two octads may be encountered in which all nuclei lie in almost the same plane, as illustrated in the photomicrograph in Fig. 66.

Whether wall formation takes place before the cells degenerate,

has not emerged from the paraffin sections. However, pollen-grains with from one to seven chromosomes could be distinctly observed in an aceto-carmine squeeze preparation in connection with the fixation.

Only one polymitotic division has been observed. The term polymitosis is thus not so suitable here, but this term of BEADLE's has been retained, as in other respects the phenomenon agrees in principle with the polymitosis of maize. In maize as many as four supernumerary divisions have been observed. The occurrence of more supernumerary divisions in maize than in *Alopecurus* may no doubt depend upon the higher chromosome number ($n = 10$) of maize.

When only a single supernumerary division occurs, as in *Alopecurus*, the phenomenon might presumably be regarded as a premature pollen mitosis after an abnormally shortened resting stage. In view of the fact that more supernumerary divisions occur in *Zea* the phenomenon seems, however, to be interpretable as due to a tendency to continuous divisions of some other kind. Under any circumstances the resting stage between second division and pollen mitosis is very short. The chromosomes are clearly undivided at metaphase. Consequently, chromosome division in II—A, as assumed by certain investigators, does not seem to occur. A clear orientation in the equatorial plane takes place, however, in contrast to the condition in absolute asyndesis. The chromosomes must, accordingly, be polarized in conformity with DARLINGTON's (1937) view. There is here an incontestable »precocity» after an extremely short resting stage. For this reason no chromosome pairing can obviously be expected, as homologous chromosomes are missing. DARLINGTON states that bivalents occur in polymitotic maize. BEADLE (1933 b) denies this himself, however, and states that no chiasmata occur during polymitosis. It would of course be extremely interesting to investigate whether there is any syndesis in the polymitosis of autotetraploid *A. myosuroides*. Autotetraploids can be easily produced by means of colchicine treatment. By using seed from a plant that is

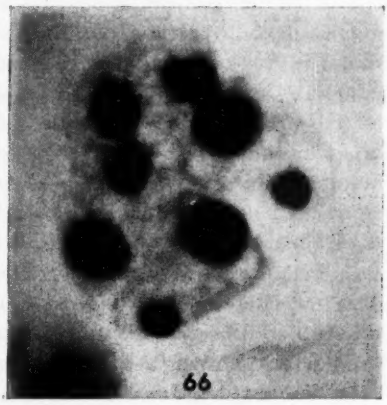


Fig. 66. Photomicrograph of an octad resulting from the polymitotic division. × 3000.

heterozygous for polymitosis it ought to be possible to obtain autotetraploid and polymitotic plants. If the chromosome pairing is a pure mechanical consequence of precocity, such plants ought to show syndesis during polymitosis and thus undergo double meiosis. If, however, the prophase pairing presupposes a complete despiralization during a long resting stage, as is maintained by SAX and SAX (1935), polymitotic pairing should not occur.

8. SYNCYTE FORMATION.

Syncytes (LEVAN, 1941) occur rather numerously in a number of plants. These giant cells may be of considerable size, and a single cell may occupy the greater portion of a loculus. The number of chromosomes in the syncytes may be several hundred, but may also be more moderate, about 50—100 and down to 28 (syndiploidy). The origin of these cells is quite clear: they are caused by failure of wall formation in the premeiotic divisions. In the meiotic prophase the syncytes contain a varying number of separate nuclei. It is characteristic of the syncytes that the condition of syndesis within these agrees with the diploid pollen mother-cells. Thus, multivalents do not occur, and if the diploid cells have a certain asyndesis frequency the syncytes also have approximately the same univalent frequency. The different nuclei therefore pass separately through the prophase stages. Not until the nucleoplasm surface is broken up do the chromosomes assemble, most often in one group forming one common metaphase plate. On account of the intense crowding this plate is often arched and angulated. A number of chromosomes can, as a rule, be seen free in the plasm outside the metaphase plate. Frequently these cells, which are always retarded as compared with normal cells, do not seem to develop beyond I—M. Occasionally, however, I—A as well as the second division may take place in a normal manner, apart from such deviations as are a direct result of the high chromosome number, e. g. excessive crowding.

There are rather many incidental reports of syncytic formation or »plasmodial masses», which term is rather apt, as the syncytes often have an irregular outline. A special description of syncytic formation has been given by LEVAN (1941) with haploid *Phleum pratense* as object of observation.

9. GENERAL DISCUSSION OF THE CYTOLOGICAL OBSERVATIONS.

Since the chief features of meiosis and microsporogenesis became known at the end of the last century, our knowledge of these processes has been steadily increasing. Of especially great value is the conception that I—M pairing is conditioned by chiasmata that have arisen during prophase, and further that the chromosome pairing at which the chiasmata are formed presupposes structural homology between chromosomes or chromosome segments. [However, the possibility that chiasmata can be formed even at non-homologous pairing cannot be flatly denied (LEVAN, 1942).] As a result of these theories, viz. that at pairing chiasmata are formed between homologous segments and that metaphase pairing is conditioned by chiasmata, a clear understanding of many deviations from normal meiosis has been obtained. For instance, it has been possible to trace the great majority of meiotic disturbances back to numerical or structural hybridity. On the other hand, a number of disturbances, certainly not so often observed but none the less important, have not admitted of being totally explained. These disturbances may be denoted as developmental-mechanical. Several examples of them have already been dealt with in this work. A full understanding of the nature of these phenomena demands a more exact knowledge of the fundamental details of chromosome mechanics than we possess at present. Above all, our deficient knowledge of the inner structure of the chromosomes, the mode of their reproduction, and the forces which initiate and direct nucleus division, is a serious obstacle to our comprehension of the developmental-mechanical disturbances.

DARLINGTON's precocity theory in explanation of the meiotic phenomena — in itself very stimulating — does not seem to be tenable. According to this theory, meiotic pairing is a mechanical consequence of a premature division after a shortened resting stage. Genically controlled absolute asynapsis would then be explained by a generally reduced precocity; partial asynapsis would depend on a reduced precocity only for certain chromosomes or chromosome segments. An equally good interpretation can be based on SAX and SAX's (1935) retardation theory. According to these authors, pairing is conditioned by the fact that at the beginning of meiotic prophase the chromosomes are completely despiralized. The pre-requisite for this despiralization is thought to be an unusually long premeiotic resting stage. On the other hand, at the commencement of mitotic prophase, pairing is considered to be prevented by the fact that the chromosomes are partially spiralized. Absolute and partial asynapsis might accordingly be due

to a generally or partially *reduced retardation.* Both these hypotheses presuppose, however, that the asynaptic metaphase chromosomes have not been paired either during prophase. This condition is not fulfilled by the asynaptic plants whose prophase stages have been observed in detail. The asynaptic chromosomes in diakinesis and metaphase have been normally paired in pachytene. The cause of failure of metaphase pairing must therefore be sought in a non-formation of chiasmata in spite of the pachytene pairing. The analysis cannot be carried further, as we do not know how chiasmata arise. Naturally enough, this fact does not invalidate either the precocity or the retardation theories. On the other hand, these theories find no support in genic asyndesis.

One of the most important characteristics of the meiotic cycle is that no centromere division occurs until II—M. This circumstance is in good agreement with the precocity theory. In the foregoing text cases of premature centromere division have been described. With the precocity theory as starting-point this premature centromere division might also be explained as a consequence of reduced precocity. In that case, as a consequence of the reduced precocity, there ought also to be asynapsis. Certainly there is partial asynapsis, but in view of the uniformity that exists at the premature division of the centromeres there should be complete asynapsis. To assume any causal connection at all between this partial asyndesis and the premature centromere division seems to be unjustifiable. With a rather high degree of probability the premature centromere division may be denoted as an independent, genotypically conditioned anomaly.

It has been definitely established that retardation of meiosis has occurred in several plants. As a consequence of this, asynapsis has not arisen, which was to be expected according to the precocity theory. To this, of course, it may be objected that the divisions have commenced with normal precocity and that the speed of division has not diminished until after pachytene. However this may be, the consequences that have attended retarded meiosis are quite explicable. The most obvious general consequence is an abnormal contraction, apparently in combination with an abnormal swelling of the chromosomes. Both phenomena can be interpreted on the basis of the longer time the internal development of the chromosomes has had at its disposal. This has allowed increased spiralization to take place, as well as probably an increase in the nucleic-acid content, which has been shown by CASPERSSON (1941) to vary during the chromosome cycle, with its lowest value in the resting nucleus and its highest in metaphase.

Other consequences of retarded meiosis have proved to be that meiosis remains in a certain condition while cytokinesis proceeds in a more or less modified form. This shows that meiosis and cytokinesis are to some extent parallel autonomous processes. However, the formation of new cell-walls is probably dependent on a normal spindle. When the spindle is incompletely developed, the cell-walls appear to be incomplete (cf. Fig. 43). Other cases of non-formation or incomplete formation of cell-walls are described by, e. g., MOFFETT (1932) in *Kniphofia*, BEADLE (1932 a) in maize and BERGMAN (1935) in *Leontodon*. Without doubt, the spindle may also vary independently of the chromosome cycle. In the case of retarded meiosis described above the retardation must be considered to depend on a retarded or incomplete formation of the spindle. A very instructive example of variations in spindle formation is also described by DARLINGTON and THOMAS (1937) in a *Festuca—Lolium* hybrid. Undoubtedly, the formation of the spindle takes place under co-operation of centra inside and outside the chromosomes, as DARLINGTON (1937) assumes. Polarized centromeres or paired chromosomes are, however, by no means a general necessity for effective spindle formation. In absolutely asyndetic *Alopecurus myosuroides*, as also in other cases of asyndesis due to various causes, the spindle is often typical in every way.

So-called stickiness is a particularly interesting phenomenon. There is here a complete disorganization of the nuclear substance, manifesting itself in abnormal interchanges of quite certainly non-homologous segments, from which follow multivalents, fragments, bicentric chromatids, and chromosome structures re-arranged in various ways. These disturbances are probably symptoms of interferences within the reproductive mechanism of the chromosomes. DARLINGTON's (1942) attempt to interpret such disturbances as a consequence of changes in the nucleic-acid metabolism is perhaps a step in the right direction.

All the abnormalities mentioned are bound up with meiosis, but there also occur premeiotic as well as postmeiotic disturbances of the microsporogenesis. A characteristic premeiotic disturbance is the syncytic phenomenon caused by failure of wall formation in archesporial divisions. In mild cases wall formation has failed only at the last premeiotic division, from which binucleate pollen mother-cells, syndiploidy, follows. As a result functional diploid gametes can certainly arise. Syndiploidy has also been indicated as a path of origin for polyploids. If wall formation fails in several consecutive archesporial divisions, the result will be polyenergid pollen mother-cells with a greater or less

number of nuclei. The resultant giant cells or plasmodial masses probably never develop functional pollen-grains.

Polymitosis represents, on the other hand, a postmeiotic disturbance of the microsporogenesis. It is here really possible to speak of precocious divisions. When the phenomenon appears in diploid organisms, no chromosome pairing is to be expected in the polymitotic divisions, of course, according to the precocity theory. Pairing would, however, take place in the polymitosis of polyploids, especially of autopolyploids. Attempts made by DARLINGTON to interpret a number of chromosome pictures in polymitotic maize as bivalents have been contested by BEADLE. A point to be observed, however, is that at the polymitotic divisions the chromosomes do not exhibit any signs whatever of longitudinal division. Any interpretation that the chromosomes already divide at anaphase is contradicted by this. Another polymitotic feature worthy of attention is that the undivided and unpaired chromosomes arrange themselves here in a perfect metaphase plate, in contrast to their behaviour at I—M in cases of absolute asyndesis. The stage of polarization of the centromeres must therefore be regarded as further advanced after the extremely short resting stage in polymitosis than after the long prophase stage in I—M. Possibly the retarded centromere polarization during meiosis also plays a part for the meiotic prophase phenomenon. On the other hand, it is conceivable that the nuclear divisions are initiated by the fact that the polarization of the centromeres has reached a certain limit and that this polarization takes place with abnormal rapidity after meiosis in polymitotic plants.

In any case, it is an indisputable fact that the successful course of microsporogenesis up to functional pollen-grains depends on a series of processes that take place before, during and after meiosis and that may be disturbed in various ways with a disastrous result. Above all, a regular meiosis implies extremely well-balanced synchronic reactions, which can be brought into disorder from various causes.

X. THE CYTOGENETICAL BEHAVIOUR OF DIFFERENT FAMILIES.

A detailed analysis is given in this section of the cytogenetical behaviour that has been found to characterize different families. For the purpose of this study families of different origin have been grouped with reference to whether crosses have been undertaken between them. The crosses have been carried out entirely at random. Hence their

joint treatment here does not imply any *a priori* agreement between the sources, whether in a morphological respect or in their cytogenetical relations.

1. 47x AND DELFT DESCENDANTS.

As previously stated, 47x is an arbitrary designation for a family of unknown origin. A parental plant of this family was included in 1936 as mother in a crossing experiment with *A. aequalis*. The progeny, which consisted of 21 plants, was completely matroclinal and thus consisted of I_1 plants. Of these plants, 16 were normal while five were absolutely ♂-sterile. One of the ♂-sterile plants was characterized by syndiploidy in high frequency, while the four others showed complete asynapsis. From 14 of the normal sister plants a new generation was raised after open pollination. In seven of the families thus obtained there appeared asynaptic plants. On the strength of this the conclusion was drawn that this asynapsis was monofactorially conditioned (JOHNSSON, 1941).

In this investigation of the cytogenetics of *A. myosuroides* seven plants belonging to the above-mentioned I_1 have been included. These plants are denoted as 0—3, 0—4, and so on. All of them were ♂-fertile. From them, firstly, successive inbred generations were raised, secondly, crosses were carried out with them as indicated in Table 4. The first column of this table contains the numbers given to the families, the second column gives their source. A designation such as 39—3 in this latter column indicates plant No. 3 from family No. 39 as the source of family 55. When only one plant is given as source, self-fertilization is at hand. Thus, after self-fertilization plant 0—4, which itself represents I_1, has given rise to family No. 17, plant 2 from this I_2 family has given the I_3 family No. 32, and plant 9 from family No. 32 has, after self-fertilization, given family No. 50, which is thus an I_4 family. The expression 15—1 × 17—2 as source of family 41 implies that this family is derived from a cross between plant 1 out of family 15 and plant 2 out of family 17, and so on. The chief purpose of the table is to give a survey of the ♂-fertility in the respective families, and data are therefore provided as to the total number of plants within each family, number of absolutely ♂-sterile plants and their meiosis, and the number of ♂-fertile plants and their percentage of morphologically perfect pollen.

An analysis of the ♀-fertility of the original plants is given in Table 5. This also gives the percentage of good pollen produced by

TABLE 4. ***The ♂-fertility of descendants of 47x.***

(A = absolute asynapsis, S = stickiness, N = normal, U = with univalents, C = with syncytes.)

Family No.	Origin	Number of plants	♂-sterile plants		Number of ♂-fertile plants	Percentage of good pollen												
			number	meiosis		37,5	42,5	47,5	52,5	57,5	62,5	67,5	72,5	77,5	82,5	87,5	92,5	97,5	Mean
14	0— 3	2	1	A															
16	0—10	3	0		3				1				1		1				68,3
19	0—2 × 0—6	12	2	S	10						1	1		4		2		2	80,5
18	0—11	25	8	4A, 2S, 2N	17				2	1		4	4	4	1	1			70,5
39	18— 4 × 18—15	28	5	S	17							1	1	2	7	2	4		83,0
40	18—15 × 18— 4	27	9	S	14							1	1		1	7	3	1	86,1
55	39—3	15	0		12						1	1			2	2	4	2	86,0
51	40—5	25	4	1S, 3A	18					1	1	2	1	1	5	1	3	3	81,4
52	40— 8 × 40— 5	4	0		4						1						3		85,3
15	0—8	4	2	U, C	2					1					1				69,5
17	0—4	5	0		5					1	2			1				1	71,0
32	17—2	31	0		27	1		4	2	2	1	3	5	3	4	2			67,3
50	32—9	14	0		12		2		1			1	2	1			2	3	75,1
41	15— 1 × 17—2	28	5	N, U	17	1		1	2	2	3	2	1	2	2	1			64,8
53	41—7	25	1		2													2	96,5
54	41—20 × 41—7	1	0		1													1	95,0
25	0—4 × Delft	9	0		8			1		2				2	2			1	71,9
24	Delft × 0—4	15	0		12				1		3		1	1	1	1	1	3	78,2
34	24— 7	27	4	N, U	10		2		1	1	2	1		1	1	1			63,1
31	25— 7	31	1	U	24			1	1	2	2	2	2	6	6	1	1		72,9
44	31— 9	25	2	S	21			2	1	1	2		3	3	2	2	4	1	75,3
43	31—15	22	0		17			1				5	3		2	3	2	1	76,6
1	Delft	7	0		7				1	1				1		1	1	2	80,7
Totals		385	44		260	2	4	10	13	15	19	24	25	32	38	27	28	23	75,75

the original plants, when this is known. The designation »st.» in the column for »% good pollen» implies that the plant in question was absolutely ♂-sterile.

The first three families in Table 4 are not continued by following generations. Family 14 from plant 0—3 comprised only two plants. The seed setting of 0—3 was only 1,7 %. One of these plants was

TABLE 5. *The ♀-fertility of descendants of 47x.*

Plant No.	I = selfed K = cross pollinated	Number of spikelets with seeds	Number of spikelets without seeds	Spikelets with seeds %	Good pollen %
0— 3	I	2	116	1,7	—
0—10	I	10	296	3,3	—
0—11	I	85	307	21,7	—
18— 4	K	122	256	32,3	52
39— 3	I	74	124	37,4	72
18—15	K	104	105	50,0	88
40— 5	I	42	124	25,3	89
40— 8	K	8	1000	0,8	st
0— 8	I	5	300	1,6	—
0— 4	I	36	286	11,2	—
17— 2	I	108	532	16,9	58
32— 9	I	48	3360	1,4	55
15— 1	K	120	240	33,3	st
41— 7	I	50	980	4,9	49
41—20	K	1	150	0,7	st
0— 4	K	116	121	49,0	—
25— 7	I	106	3000	3,4	55
31— 9	I	50	1300	3,7	48
31—15	I	22	2486	0,9	57
Delft	K	109	69	61,2	—
24—7	I	113	1990	5,4	54
Delft	I	9	270	3,1	—

completely asynaptic, from the other no pollen samples were obtained. Whether it was absolutely ♂-sterile, however, has not admitted of being definitely established. Nor has the meiosis been studied. The original plant, 0—3, must at all events be heterozygous for asynapsis.

The original plant of family 16, 0—10, was also extremely self-sterile. The three daughter plants were ♂-fertile with varying percentages of good pollen. Meiosis was quite regular in all of them. For the intercross 0—2 × 0—6 there are no data as to ♀-fertility.

TABLE 4. *The ♂-fertility of descendants of 47x.*

Of 12 daughter plants from 0—2, ten were ♂-fertile and 2 completely ♂-sterile. In the ♂-fertile plants the percentage of good pollen lies between 64 % and 99 %, with an average of 80,5 %. Meiosis was examined in 9 of these plants, but no deviations from the normal were found. The two ♂-sterile plants showed typical stickiness.

Isolation of a ♂-sterile sticky plant together with a ♂-fertile plant with 66 % good pollen did not result in any seed setting in either the ♂-sterile or the ♂-fertile plant.

The next section of Table 4 includes six families derived from the I_1 plant 0—11. Family 18, I_2, comprises 25 plants, 17 of which were ♂-fertile and 8 ♂-sterile. On commencing to flower all the plants appeared to be ♂-sterile, the anthers not opening in any of them. However, microscopical examination of the anthers showed that they often contained a large quantity of good pollen. In 17 of the plants, in fact, the anthers contained good pollen in varying frequencies. Later on in the flowering stage pollen was, indeed, normally discharged by these plants. The anthers of the remaining eight plants contained exclusively empty pollen-grains at the beginning of the flowering stage, and these plants subsequently remained ♂-sterile. Meiosis was studied in 24 plants. It was almost entirely regular in the 16 ♂-fertile plants examined. In five plants, however, syncyte formation was found in varying frequency, and in two plants two univalents occurred, though rarely. Of the absolutely ♂-sterile plants two showed regular meiosis, two had sticky meiosis, and four were asynaptic. Plant 0—11 was thus heterozygous for both asynapsis and stickiness.

The two families 39 and 40 consist of two reciprocal crosses between two plants from the preceding I_2 family. The families agree fully with each other; both segregate out sticky plants in high frequency and both must therefore be heterozygous for stickiness.

One plant from each of these two cross families was self-fertilized. Plant 39—3 gave 12 ♂-fertile daughter-plants with a determined percentage of good pollen. The family comprised another three plants. Of these, one was fertile, one died before flowering, and in one the ♂-fertility could not be determined with certainty. Plant 40—5 had among a total of 25 daughter-plants 18 ♂-fertile and four ♂-sterile plants. Of the remaining three plants, two died before flowering and the fertility of the third is unknown. Of the four ♂-sterile plants, three were asynaptic and one sticky. The fact that asynapsis occurs in this family must mean that one of the plants 18—4 and 18—15 was heterozygous for asynapsis.

The parental plant of the preceding inbred family was also used as father plant in an intercross with a ♂-sterile sticky sister plant. The seed setting here was very low and only four plants could be raised. These were all ♂-fertile.

The following seven families in Table 4 were derived from plants 0—8 and 0—4. Families 15 and 17 are the I families of the respective plants. Both 0—8 and 0—4 were highly self-sterile, and therefore only a few daughter plants were obtained from each, four from 0—8 and five from 0—4. Of the four plants in family 15, two were ♂-sterile. In one of them meiosis was perfectly regular, in the other solitary univalents could be observed. One of the two ♂-fertile plants showed a distinct univalent frequency:

No. of univalents per PMC	0	2	4
No. of PMC's	33	14	2

This frequency works out at 0,7 univalents per PMC. In addition, syncytes occur in high frequency.

The five plants within family 17 were all ♂-fertile and had normal meiosis. One of the plants, which had 58 % good pollen, was selfed and as a result gave rise to family 32. Of the 31 plants belonging to this family, 27 were ♂-fertile. Three of the remaining four plants died before flowering, and the fertility could not be determined in the fourth. From this family, too, one plant was selected for selfing. The plant in question had only 55 % good pollen. The family established in this way, No. 50, comprised 14 plants. The pollen fertility is given for 12 of these, while two did not develop panicles.

One of the ♂-sterile plants with regular meiosis out of family 15 was intercrossed with a plant out of family 17, plant 2, which at the same time had given the above-mentioned inbred family No. 32. The cross was relatively fertile, and a progeny of 28 plants could be raised. As regards ♂-fertility, the family has the following composition: 17 ♂-fertile, 5 ♂-sterile, 2 dead, 4 unevaluated plants. Meiosis was studied in three of the ♂-sterile, five of the ♂-fertile, and in one of the unevaluated plants. One ♂-sterile plant showed a low but distinct univalent frequency, the two others were regular. The ♂-fertile plants examined, which had respectively 49, 57, 64, 75 and 75 % good pollen, exhibited perfectly regular microsporogenesis. The plant whose ♂-fertility could not be determined possessed a relatively high univalent frequency, viz.

No. of univalents per PMC	0	2	4	6	8
No. of PMC's	15	10	9	0	1

The average is 1,8 univalents per PMC. Further, at I—A there occurred, though rarely, bicentric chromatids with fragments, in addition to which a trivalent was found.

Plant No. 7, which had 49 % good pollen, on self-fertilization gave rise to family 53. This family, which originally comprised 25 plants, was vegetatively very feeble indeed and no fewer than 16 plants died before flowering. Of the remaining nine plants, seven were with certainty ♂-fertile. Pollen samples were only obtained from two, however. One plant was ♂-sterile. Fixation of this was, however, unsuccessful. The ninth plant produced only one panicle. This was fixed, and microsporogenesis was found to be normal. One ♂-fertile plant examined also showed an entirely regular meiosis.

One of the ♂-sterile plants, No. 20 from family 41, was intercrossed with the fertile sibling plant, which on self-fertilization gave family 53. The ♀-fertility was also very low, and only a single plant was obtained from the cross. This plant possessed exceedingly good pollen.

The last section of Table 4 contains seven families derived from 0—4 and Delft.

All 47x descendants agree morphologically and are medium-strong, few-leafed, many-strawed, and early plants. The I_1 of Delft is also very much like the 47x families. The relative vegetative development of the different families is indicated in Table 6.

The hybrid families between 0—4 and Delft also agree in general type with the two parents.

The F_1 families 24 and 25 did not show any ♂-sterile plants. The proportion of good pollen in the ♂-fertile plants was on an average between 70 and 80 %, with a variation from 49 % to 99 %. All the plants except one of family 24 were cytologically examined. As previously mentioned, no disturbances of any kind were observed in this family. Within family 25 meiosis was only studied in one plant, that with the lowest percentage of good pollen, viz. 49 %. The only disturbance that occurred consisted in the appearance of two univalents in solitary PMC's. Self-fertilization of this plant gave family 34. Of the 27 plants originally constituting this family, nine died before flowering. The vitality of the family was therefore low. Pollen samples were obtained from ten plants, while absolute ♂-sterility could be definitely established in four. The other four more or less weak plants

did not flower at all, or only sparingly. Of the four ♂-sterile plants, one had a perfectly regular meiosis, one had an occasional PMC containing two univalents, and one showed a somewhat higher univalent frequency, about one PMC in ten having two univalents. The fixation of the fourth plant contained only young tetrads, which, however, were completely regular. Two ♂-fertile plants with respectively 40 % and

TABLE 6. *Vitality of descendants of 47x.*

Family No.	Origin	Number of plants				
		Robust	Normal	Weak	Very weak	Dead
14	0— 3		1	1		
16	0—10		3			
19	0— 2 × 0— 6	2	10			
18	0—11		20	5		
39	18— 4 × 18—15		28			
40	18—15 × 18— 4		26			1
55	39— 3	1	12	1		1
51	40— 5		22	1		2
52	40— 8 × 40— 5	1	2	1		
15	0— 8		2	2		
17	0— 4		5			
32	17— 2		28			3
50	32— 9		7	2	1	4
41	15— 1 × 17— 2		23		3	2
53	41— 7	1	6	1	1	16
54	41—20 × 41— 7			1		
25	0— 4 × Delft	2	6	1		
24	Delft × 0— 4	5	10			
34	24— 7		14	2	2	9
31	25— 7		28	2	1	
44	31— 9	4	16	1	3	1
43	31—15	6	10		3	3
1	Delft	3	4			

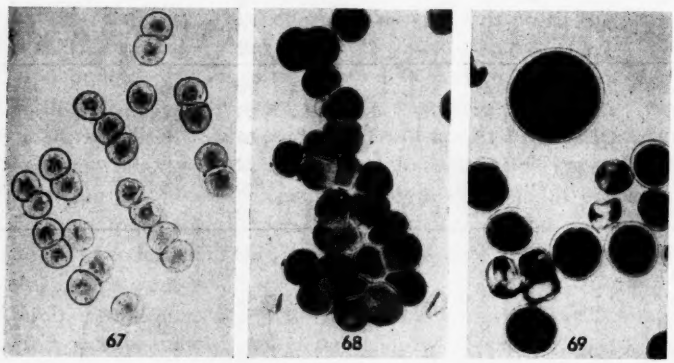
53 % good pollen were also cytologically examined. Both had quite regular meiosis.

One plant from the reciprocal cross was also self-fertilized. This family bears the number 31. Of the plants composing the family, 24 were ♂-fertile and one ♂-sterile, while the fertility could not be definitely fixed in six plants. Meiosis was studied in one of these six. Slight disturbances were present in the form of solitary pairs of univalents and, rarely, bicentric chromatids with fragments in I—A and

II—A. In the ♂-sterile plant, too, univalents occasionally occurred, but no other irregularity. Two plants with respectively 57 % and 78 % good pollen had regular meiosis.

The pollen-grains in all the ♂-fertile plants of the family displayed a clear tendency to hold together in pairs, as indicated in Fig. 67. In one plant this tendency was intensified, so that veritable pollinia appeared in the flying pollen, as illustrated in Fig. 68. The pollen from two plants contained gigas grains in considerable frequency (Fig. 69).

Two plants out of the I_1 family last treated were selfed and are the parents of the two I_2 families 43 and 44. Family 43 comprised 22



Figs. 67—69. Photomicrographs of pollen samples from three different plants belonging to family No. 31. — Fig. 67. Pollen grains, connected in pairs from plant 15. × 200. — Fig. 68. Pollen grains connected in large masses from plant 16. × 250. — Fig. 69. Pollen sample with giant grain from plant 9. × 300.

plants, from 17 of which pollen specimens were obtained, while three of the plants died before flowering and two weak plants entirely failed to flower. One of the fertile plants was cytologically studied. This plant had 68 % good pollen. Meiosis was regular, but numerous and sometimes very large syncytes occurred.

Among a total of 25 plants there are 21 ♂-fertile and two ♂-sterile plants in family 44. Besides these, one plant died before flowering and one plant did not flower. Both the ♂-sterile plants showed typical stickiness. One of the fertile plants (49 % good pollen) possessed gigas grains in considerable frequency, but no peculiarities in meiosis associated with this could be observed.

The original Delft plant was very self-sterile. The small I_1 family

which could be obtained, and which bears the number 1, comprised only 7 plants, which were all ♂-fertile.

The descendants of 47x and Delft thus gave altogether 44 absolutely ♂-sterile plants in 12 families. These 12 families further had altogether 152 verified ♂-fertile plants, the *fertile* : *sterile* ratio thus being 152: 44, which corresponds closely to the 3 : 1 ratio, which on a total of 196 individuals gives 147 : 49. Beyond all doubt, the ♂-sterile plants also represent recessive segregation products. They belong, however, to three different categories, viz. asynaptic plants, sticky plants, and plants without or with slight meiotic disturbances. The question is whether all these three types are mono-factorial. An analysis of the composition of the different families is given below:

Family No.	14	19	18	39	40	51	15	41	53	34	31	44
No. of fertile plants	0	10	17	17	14	18	2	17	2	10	24	21
» » asynaptic plants..	1	0	4	0	0	3	0	0	0	0	0	0
» » sticky plants	0	2	2	5	9	1	0	0	0	0	0	2
» » ♂-sterile plants without major meiotic disturbances	0	0	2	0	0	0	2	5	1	4	1	0

The three families with asynaptic plants gave *no asynapsis* : *asynapsis* = 40 : 8, while 3 : 1 corresponds to 36 : 12. However, as the mean error is 3,0, the numerical ratio found does not contradict a monohybrid segregation. Monohybrid segregation of »asynapsis» is, in fact, supported by previously published results (JOHNSSON, 1941).

Stickiness occurred within six families, with altogether 21 sticky and 106 non-sticky plants. Monohybrid segregation would give 95,25 : 31,75, with a mean error of 4,9, as against the actual ratio 106 : 21. Here, too, there was thus a monohybrid segregation. However, the frequency of sticky plants was rather different within different families. Families 39 and 40 (reciprocal crosses) had sticky plants in a considerably higher frequency than the rest. Here there were altogether 14 sticky plants and 31 normal. The theoretical numerical ratio in monohybrid segregation would be 33,75 *normal* : 11,25 *sticky*, with a mean error of 2,9. No other interpretation than a 3 : 1 segregation for these two families is probable. The other three families with sticky plants had, however, the following proportions of non-sticky to sticky: 10 : 2, 23 : 2, 21 : 1, 21 : 2, or altogether 75 : 7. The theoretical numerical ratio in monohybrid segregation is 61,5 : 20,5, with a mean error of 3,9.

Monohybrid segregation must therefore be regarded as very improbable here. Instead, it is far more probable that the segregation was dihybrid and that the sticky plants consisted of double recessives. The theoretical numerical ratio would then be 76,9 : 5,1 as against the actual 75 : 7. On this assumption the agreement is thus very good. It must then be thought that stickiness is governed by two recessive factors, s_1 and s_2, which separately do not affect meiosis in either the heterozygous or the homozygous condition, nor together, when both or either of them are heterozygous. If they are both in the homozygous condition, stickiness occurs. The parent plants of families 18, 19, 44 and 51 must therefore have been heterozygous for both the factors, while the parent plants of the families 39 and 40 must have been homozygous for one factor and heterozygous for the other.

Also in the case of ♂-sterility unconnected with major meiotic disturbances the numerical ratios found are in agreement with those expected in monohybrid segregation. Such ♂-sterile plants are found within six families to a total number of 15 as against 78 normal or ♂-sterile plants from the above-mentioned causes. The theoretical ratio is 69,75 : 23,25 with a mean error of 4,2. For this category also, however, the frequency of abnormal plants varies between the families. Within families 18 and 31 the frequency is low and in better agreement with dihybrid segregation, while the frequency within the rest of the families is higher, pointing to monohybrid segregation. Probably, however, this category is not uniform. All the plants certainly possessed the common feature that the pollen aborted after a regular microsporogenesis. In all probability this pollen destruction was genotypically conditioned, but the physiological course of the abortion as well as the factorial basis may have been different within different families.

With regard to the segregation of the different factors for sterility it is clear that plant 0—11 was heterozygous for both asynapsis and stickiness. One of the daughter-plants which had given rise to families 39 and 40 was heterozygous for asynapsis, but the other was not. Asynapsis, thus, did not occur within these families, although half the plants must have been heterozygous for the asynapsis factor, among them plant 5 in family 40, from which family 51 was derived; though probably not plant 8 in the same family and nor plant 3 in family 39.

The sticky factors realized in family 44 were probably introduced via plant 0—4. The fact that on self-fertilization plant 0—4 did not give sticky plants can scarcely mean anything, since the I_2 family did

not comprise more than five examined plants, and the plant that had been arbitrarily chosen as parent to I_3 obviously need not have been heterozygous. Since stickiness segregates out in family 44, the original plant of this family, No. 9 from family 31, must have been heterozygous. Stickiness ought therefore to have also appeared in family 31. This was not the case, however. Still, it is not surprising that a type expected in a frequency of 1 in 16 failed to appear in a progeny of only 25 examined plants.

Only a small part of the ♂-fertile plants produced fully good pollen containing but few empty grains.

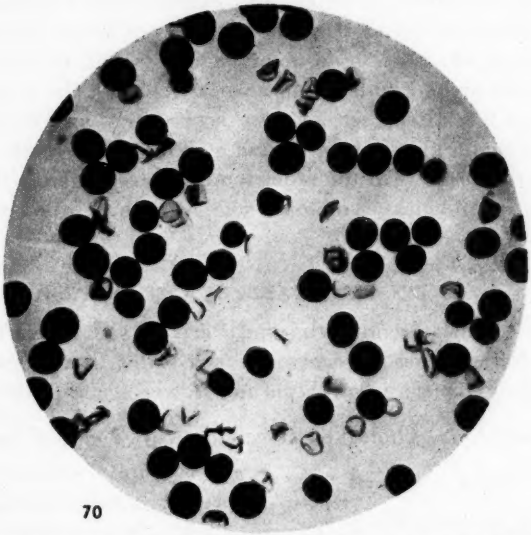


Fig. 70. Photomicrograph of a pollen sample, showing the sharp boundary between good and poor grains. × 150.

Most of the plants showed a more or less reduced pollen vitality. In some, 50 % and even more of the pollen-grains were empty. The average good pollen for all the 260 fertile plants was 75,75 %. Remarkably enough, nearly all the cytologically examined plants with reduced pollen vitality showed no meiotic disturbances whatever. Very rarely there was a slight univalent frequency. The difference between good and empty pollen-grains was almost always perfectly sharp, as shown in Fig. 70. Only in exceptional cases was there a continuous transition between good and empty grains.

Significant differences in pollen vitality undoubtedly occurred between different families. The six families derived from plant 0—11 had on an average 81,5 ± 1,3 % good pollen, while the seven families derived from plants 0—4 and 0—8 averaged 69,9 ± 2,1 % good pollen. The seven families originating from the cross 0—4 × Delft had 74,5 ± 1,5 % good pollen and thus these also showed significantly lower pollen vitality than the 0—11 families.

In the ♂-fertile plants no distinct correlation could be found between percentage of good pollen and seed setting after self-fertilization or crossing, as Table 5 shows. The absolutely ♂-sterile plants with asynapsis or stickiness, however, also exhibited an extremely reduced ♀-fertility. Thus, in asynaptic plants seed setting never occurred. From sticky plants it was possible to obtain solitary seeds, but the ♀-fertility was extremely low. Plants 40—8 and 41—20 in Table 5 with respectively 0,8 and 0,7 % seed setting were accordingly sticky plants. It is therefore probable that asynapsis and stickiness also assert themselves in megasporogenesis. On the other hand, ♀-sterile plants that are free from special cytological symptoms sometimes have good seed setting, e. g. plant 15—1 in Table 5.

2. JENA AND PARIS DESCENDANTS.

The I_1 families having Jena and Paris as sources agreed in habit and were characterized by vigorous, many-leafed, few-strawed and late plants, among which a number did not flower at all or very sparingly.

TABLE 7. *Vitality of descendants of Jena and Paris.*

Family No.	Origin	Number of plants				
		Robust	Normal	Weak	Very weak	Dead
13	Jena	19	5			1
35	13— 5		24			4
46	35—15		12	8	4	1
47	35—18	4	2	1		
11	Paris	17	6	2	1	1
38	11—11	4	24		1	
50	38—15	4	7	2	1	
28	Jena × Paris	11				
29	Paris × Jena	8		3		

They are illustrated rather well by Fig. 7 *c*. The F_1 families between the two sources also belonged to this type. In later inbred generations vigorous, many-leafed and few-strawed plants were common, though weak and sublethal plants also appeared among them, as indicated in

Table 7. From the two sources, I_1, I_2 and I_3 families were raised, as shown in Table 8, which gives a survey of the ♂-fertility within the different families.

Family No. 13, which represents the I_1 of Jena, comprised 25 plants. It was possible to determine the fertility in 18 of these, while the other seven did not flower until the coming of autumn. No ♂-sterile plant could be detected. Some of the fertile plants had low pollen vitality. The two plants that had the lowest percentage of good pollen were cytologically studied. In neither of them was there any essential meiotic disturbance, although a certain instability could be observed. This consisted in the occurrence of two univalents in solitary PMC's.

The I_2 family, No. 35, originally consisted of 28 plants, but four feeble plants among these died before flowering. No pollen samples could be obtained from five plants on account of their failure to flower. Of the remaining 19 plants, 16 were found to be fertile and three ♂-sterile. The ♂-sterile plants had complete asyndesis.

TABLE 8. *The ♂-fertility of descendants of Jena and Paris.*

(A = absolute asynapsis.)

Family [No.	Origin	Number of plants	♂-sterile plants number meiosis		Number of ♂-fertile plants	Percentage of good pollen														Mean
						37,5	42,5	47,5	52,5	57,5	62,5	67,5	72,5	77,5	82,5	87,5	92,5	97,5	
13	Jena	25	0		18	1	1			1		1	2	3	3		4	2	77,2
35	13— 5	28	3	A	16								1	2	5	5	3		84,3
46	35—15	25	6	A	10						1					4	3	2	88,6
47	35—18	7	1	A	5									1		1	2	1	88,8
11	Paris	27	0		17		1					1	1	2	1	1	1	9	87,0
38	11—11	29	0		25				2			1	1	5	3	7	4	2	81,6
50	38—15	14	0		12		2		1			1	2	1			2	3	75,1
28	Jena × Paris	11	0		4										2	1		1	86,5
29	Paris × Jena	11	0		4			1								2	1		78,3
Totals		178	10		111	1	4	1	3	1	1	4	7	14	14	21	20	20	82,8

From this I_2 family two I_3 families were raised from plants 15 and 18. Family 46, which consisted of 25 plants, was very variable in habit. Twelve plants were recorded as vegetatively normal, eight as weak, and four as very weak, in addition to which one plant died at a very early age. The 12 vegetatively normal plants were composed of seven ♂-fertile and five ♂-sterile. The eight weak plants consisted of two fertile and one sterile plant as well as five plants that failed to flower. On cytological examination three of the last-mentioned were found to have regular meiosis, while the other two did not produce panicles. From one of the four very feeble plants pollen specimens could be obtained. The other three did not flower. One of them, however, could be fixed and proved to be weakly asynaptic, the univalent frequency being as follows:

No. of univalents per PMC	0	2	4
No. of PMC's	24	18	8

This frequency corresponds to 1,36 univalents per PMC.

All the six ♂-sterile plants were asynaptic, one of them not so completely as had otherwise always been the case. Solitary bivalents occurred, as previously described on p. 488. A certain syndiploidy frequency was also characteristic of the asynaptic plants of the family.

The sister family, No. 47, consisted only of seven plants. Of them, five were ♂-fertile and one ♂-sterile. The ♂-sterile plant was asynaptic.

Thus, 31 fertile and 10 asynaptic plants occurred in the I_2 and the two I_3 families, a proportion that agrees as closely as is conceivably possible with that required by a 3 : 1 segregation.

Since the I_2 and I_3 segregated into asynaptic and normal plants, there should also have been the same segregation in the I_1. The I_1 consisted of 18 plants of known fertility. On probability grounds one or more asynaptic plants ought to have appeared among these 18. The probability that no recessive segregates out among 18 individuals in a monohybrid segregation is only 6 in 1000. Hence such a rare case seems to be present here.

Other hypotheses, however, can be set up to explain the absence of recessives in the I_1.

Family 11, which represents the I_1 of Paris, is for the most part made up of vigorous plants, though some weak ones also occurred, one of which died before flowering. The ♂-fertility could be determined

in 17 plants, while nine failed to flower. Meiosis was only studied in one plant, that with the lowest percentage of good pollen, 41 %. On the whole, meiosis proceeded without disturbances. Solitary PMC's with univalents occurred, however. At I—A there was also a bicentric chromatid with fragment in about 1 PMC in 10. Bicentric chromatids could also be observed at II—A now and then. No ♂-sterile plants appeared in this I_1 or in the I_2 or I_3, families No. 38 and No. 50. Two I_2 plants with respectively 83 % and 68 % good pollen were cytologically studied. Both were completely regular.

TABLE 9. *The ♀-fertility of descendants of Jena and Paris.*

Plant	I = selfed K = cross pollinated	Number of spikelets with seeds	Number of spikelets without seeds	Spikelets with seeds %	Good pollen %
Jena	I	202	289	41,1	
13— 5	I	127	783	14,0	92
35—15	I	62	565	9,9	83
35—18	I	26	1820	1,4	—
Paris	I	458	322	58,7	
11—11	I	284	494	36,5	87
38—15	I	21	510	4,0	52
Jena	K	190	76	71,4	
Paris	K	165	168	49,5	

The two F_1 families 28 and 29 were chiefly characterized by their disinclination to flower, or in any case by not flowering until late in the autumn. Pollen samples were therefore only obtainable from altogether eight plants. The frequency of good pollen was high in seven of these, while one may be described as semi-sterile.

The pollen vitality was comparatively high in these families and fairly concordant in the Jena as well as the Paris descendants. The total average amounts to 82,8 %.

The seed yield of the original plants of the different families can be seen from Table 9. The ♀-fertility drops here in the successive inbred generations.

3. RENNES AND ROUEN DESCENDANTS.

The I_1 families from these two sources were on the average weak in vegetative development but varied greatly in vitality. They are illustrated in Figs. 6 *a* and 6 *c*. The F_1 between the sources was more uniform and stronger, as indicated in Fig. 6 *b*. Broadly viewed, the

successive inbred generations were of the same stamp as the I_1 families but in a number of cases were still weaker than these. The relative plant development is indicated in Table 10.

From the two sources, I_1, I_2 and I_3 families were raised (see Table 11). The great difference between the total number of plants and the number recorded as ♂-sterile and ♂-fertile is explained partly by the death of rather many plants before flowering, partly — and principally — by the fact that many small and feeble plants never developed panicles.

TABLE 10. *Vitality of descendants of Rennes and Rouen.*

Family No.	Origin	Number of plants				
		Robust	Normal	Weak	Very weak	Dead
12	Rennes	5	8	11	1	
30	12— 4		1	24		1
42	30—12	2		9	6	8
4	Rouen		3	4	2	
36	4— 7		6	15	5	4
48	36— 3	1	15	7	1	1
27	Rennes × Rouen		7	3		
26	Rouen × Rennes		12			

The I_1 of Rennes, family No. 12, comprised 25 plants. Of them, two were ascertained to be ♂-sterile, while pollen samples were obtained from 14. The remaining nine did not flower. Seven of them, however, developed panicles, so that it was possible to carry out PMC fixations. Small, feeble plants were often seen to shoot rather many panicles. Not infrequently, however, the panicles ceased to develop after microsporogenesis. The straw did not stretch, and usually only the top of the panicle shot out a little from the sheath after a long time. The anthers had then long since degenerated. Altogether 21 plants were fixed, but one of the fixations did not contain any divisions. Hence meiosis and microsporogenesis were studied in 20 plants, five of which failed to flower. Three of the non-flowering plants had regular meiosis, one showed a distinct univalent frequency, in addition to which solitary bicentric chromatids and fragments occurred. In the fifth plant of this category there was rather a high univalent frequency, viz.

No. of univalents per PMC	0	2	4	6
No. of PMC's	31	25	13	5

This represents an average of 1,8 univalents per PMC.

In four of the 13 ♂-fertile plants examined there was a low univalent frequency, in three solitary bicentric chromatids and fragments

could be observed, while in the remaining six meiosis was free from any aberrations.

Although a certain amount of cytological instability was thus detected, there were no meiotic disturbances of such a nature as to provide a direct explanation of the low pollen vitality.

The two absolutely ♂-sterile plants showed the typical retarded meiosis described on p. 497.

In all the plants examined the contraction of the chromosomes at I—M was found to be abnormally great, as described on p. 495, and in one plant the contraction was also abnormal at the second division.

The vegetatively weak I_2 family, No. 30, comprised 26 plants. Pollen samples could only be obtained from 16 plants. One plant died at an early stage. Some of the remaining 9 plants produced panicles, which underwent microsporogenesis in spite of their never having reached the flowering stage. Meiosis was studied in five of these. Three were perfectly regular, while two univalents

TABLE 11. *The ♂-fertility of descendants of Rennes and Rouen.*

(R = retarded meiosis, N = normal, S = sticky.)

Family No.	Origin	Number of plants	♂-sterile plants		Number of ♂-fertile plants	Percentage of good pollen																
			number	meiosis		27,5	32,5	37,5	42,5	47,5	52,5	57,5	62,5	67,5	72,5	77,5	82,5	87,5	92,5	97,5	Mean
12	Rennes	25	2	R	14				1			1	5		4	2	1				66,7
30	12—4	26	0		16	1							1	2		5	2	3	2		75,9
42	30—12	25	0		2													2			87,5
4	Rouen	9	0		6						1	1			1			1	1	1	75,8
36	4—7	30	6	R	6					1			1			1		3			74,5
48	36—3	25	3	N, S.	11				1					1	2	2	2	1	1	1	76,5
27	Rennes × Rouen	10	0		8												1		3	4	92,5
26	Rouen × Rennes	12	0		11											1			7	3	91,3
	Totals	164	11		74	1	0	0	2	1	1	2	7	3	7	11	6	10	14	9	79,3

occasionally occurred in the two others. All possessed the abnormally great chromosome contraction characteristic of the I_1.

The I_8 family, No. 42, was extremely feeble except for two plants, which were exceptionally vigorous. Only these two flowered. Of the other 23 plants, eight died at an early stage, while the survivals showed extremely feeble development. A few of them produced panicles, but none flowered. Meiosis was studied in four plants and proved to be regular or almost regular. In one plant no disturbances whatever could be observed, in the other three there occurred two univalents in solitary PMC's, besides which occasional bicentric chromatids with fragments were found. All exhibited abnormally great chromosome contraction.

The I_1 family of Rouen, No. 4, comprised only nine plants. Six of these yielded pollen. Meiosis was studied in six plants, among them one that had not flowered. In all of them the meiosis was of regular character, but as in the Rennes descendants the contraction of the chromosomes was abnormally great. The I_2 family, No. 36, was very weak. Of the originally 30 plants, four died very early. Only 12 plants flowered. Of them, six were fertile and six sterile. The sterile plants were characterized by retarded meiosis of the same type as in family No. 12. Three of the fertile and one of the non-flowering plants were cytologically studied. All these were normal but showed abnormal chromosome contraction.

The succeeding I_3 family, No. 48, was also weak, with a number of plants on the borderline of viability. Pollen samples could be obtained from 11 plants, and three could be definitely determined to be ♂-sterile. One of the sterile plants had a completely regular meiosis. Another showed manifest though low univalent frequency as well as, rarely, bicentric chromatids at anaphases. The third ♂-sterile plant presented different meiotic pictures at different loculi. At some loculi meiosis was regular, at others it showed a typical stickiness. One ♂-fertile plant with 71 % good pollen possessed an exceedingly regular meiosis, apart from a couple of bicentric chromatids which were observed at II—A. Four non-flowering plants were also cytologically studied. Meiosis was regular in all of them. In all the plants examined the abnormally strong chromosome contraction characteristic of these families was present.

The two F_1 families, 26 and 27, were normal in habit and of medium vigour, as shown in Fig. 6 *b* and Table 10. Pollen samples could be collected from all plants but three. The quality of the pollen

was decidedly better than in the inbred families, and no ♂-sterile plants could be detected. Meiosis was studied only in two plants. Both were normal, though they also had chromosomes that at I—M contracted to an abnormal degree.

Thus, weak vegetative development and abnormal chromosome contraction are especially characteristic features of the Rennes and Rouen descendants. It is not clear whether there is any causal relation between these two phenomena. The F_1 families, which are vegetatively normal, seem in spite of this to have an abnormal contraction. Within the I_1 of Rennes and the I_2 of Rouen there segregate plants with retarded meiosis. The development of this aberrant meiosis is on the whole the same in the two families. Therefore, the assumption is justifiable that the genotypical background in both cases is the same. Within

TABLE 12. *The ♀-fertility of descendants of Rennes and Rouen.*

Plant	I = selfed K = cross pollinated	Number of spikelets with seeds	Number of spikelets without seeds	Spikelets with seeds %	Good pollen %
Rennes	I	403	104	79,5	
12— 4	I	120	390	23,5	55
30—12	I	165	300	35,5	78
Rouen	I	21	298	6,6	
4— 7	I	100	651	13,3	99
36— 3	I	100	490	16,9	78
Rennes	K	207	57	78,4	
Rouen	K	80	44	64,5	

family 12 the ratio between plants with normal and retarded meiosis is 20 : 2, and within family 36 it is 7 : 6. In both cases the deviation from 3 : 1 is rather wide but by no means inordinate. The theoretical ratio for monohybrid segregation for 22 individuals is 16,5 : 5,5, with a mean error of 2,03, and for 12 individuals 9,75 : 3,25, with a mean error of 1,56. The actual proportions thus fall within the limits of error. If both families are combined, the *normal meiosis* : *retarded meiosis* ratio will be 27 : 8, which agrees very closely with 3 : 1. It therefore seems probable that retarded meiosis is also mono-factorially conditioned. As plants with retarded meiosis occurred within the I_2 family No. 36, the same ought to have been the case within the I_1 family No. 4. The ♂-fertility here, however, is only known for six plants, and among six individuals no recessive is to be expected at monohybrid segregation in 17 cases out of 100.

Respecting the three ♂-sterile plants in family 48, it cannot be

considered as settled that it is the same genotypical cause that is operative in all. The course of meiosis, which at all events does not deviate sharply from the regular, is not quite the same in these plants. The frequency of ♂-sterile plants found within the family points however to a 3 : 1 segregation.

The pollen vitality within the inbred families varies within wide limits, and the averages for the families indicate quarter sterility. In these families, too, there is no quantitative agreement between meiotic course and pollen lethality, all the ♂-fertile plants examined showing a fully regular meiosis, or in any case a meiosis with only slight disturbances.

Data respecting the ♀-fertility of the original plants of the families are furnished in Table 12.

4. TABOR AND MÜNCHEN DESCENDANTS.

The I_1 families with Tabor and München as sources were very unlike one another in habit. Tabor represents a few-leafed, many-strawed and early type, as seen from Fig. 7 *a*, while München represents a many-leafed, few-strawed and late type (Fig. 7 *c*). Within both families there was an essential variation in relative vigour, as is evident from Table 13. The reciprocal crosses, which are illustrated in Fig. 7 *b*, presented an example of extravagantly powerful plants.

TABLE 13. *Vitality of descendants of Tabor and München.*

Family No.	Origin	Number of plants				
		Robust	Normal	Weak	Very weak	Dead
9	Tabor	6	15	1	3	
10	München	10	1	5	2	
23	Tabor × München	15	1			
22	München × Tabor	15	2			

From both sources there were only the I_1 and the reciprocal cross families indicated in Table 14.

The I_1 family of Tabor, No. 9, comprised 25 plants. Of these, 12 plants were ascertained to be ♂-sterile. Pollen samples were obtained likewise from 12 plants. The remaining plant was also fertile and was used as mother plant for an I_2.

Detailed data regarding the fertility and microsporogenesis within the family are provided in Table 15. This table shows that the sterile plants fall within six different classes in regard to microsporogenesis.

In one plant most of the pollen mother-cells degenerated as early as during prophase. At a few loculi only, solitary PMC's were found at I—M and I—A. The chromosomes were here greatly contracted. The pollen mother-cells were, also here, cytokinetically in a far more advanced stage than is normal for the first division. It is therefore probable that this plant represents an extreme case of retarded meiosis. A typical and clear case of retarded meiosis was found in a ♂-sterile sister-plant. The latter also had a low univalent frequency, with on the average 0,56 univalent per PMC. The ♀-fertility of both these plants was very small or nil (Table 15). The figures in this table showing the percentage of spikelets with seeds relate to the seed setting at open pollination.

Three ♂-sterile plants were characterized by strong partial asyndesis, as seen below.

Plant No.	No. of univalents per PMC								
	0	2	4	6	8	10	12	14	M
13 . . .	0	3	1	8	11	10	7	9	9,31
14 . . .	1	1	4	2	8	5	5	11	9,68
21 . . .	5	24	23	25	14	2	5	2	5,10

The ♀-fertility of these plants was very variable. Plant No. 13 had good fertility, No. 14 poor, and No. 21 very poor.

Three other ♂-sterile plants exhibited only minor meiotic disturbances consisting in a low univalent frequency and bicentric chromatids with fragments. The univalent frequency in these plants was as follows:

TABLE 14. *The ♂-fertility of descendants of Tabor and München.*
(R = retarded meiosis, P = partial asynapsis.)

Family No.	Origin	Number of plants	♂-sterile plants		Number of ♂-fertile plants	Percentage of good pollen														Mean
			number	meiosis		42,5	47,5	52,5	57,5	62,5	67,5	72,5	77,5	82,5	87,5	92,5	97,5	
9	Tabor	25	12	see Table 15	12			1	2	1	2	3	1	1	1			68,4
10	München	18	3	R	9				1			1	1	1	1	2	2	84,6
23	Tabor × München	16	1	P	10			1				3		2			4	82,6
22	München × Tabor	17	0		13	1	1					1	2	3	2		3	80,2

Plant No.	No. of univalents per PMC 0	2	4	M
1	51	14	1	0,48
10	20	7	4	0,97
25	40	10	0	0,40

Especially in plant No. 1 bicentric chromatids with fragments were rather frequent.

The two ♂-sterile plants No. 8 and No. 11 showed the premature centromere division described on p. 492. A rather considerable univalent frequency also occurred in these plants, as already stated above.

TABLE 15. *Fertility and microsporogenesis within family 9.*

Plant No.	Good pollen %	Spikelets with seeds %	Microsporogenesis
12	sterile	1,4	PMC's degenerate at prophase
16	»	0,0	Retarded meiosis
13	»	42,0	Strong, partial asynapsis
14	»	4,6	» » »
21	»	0,5	» » »
1	»	0,0	Weaker aberrations
10	»	30,6	» »
25	»	8,3	» »
8	»	0,0	Precocious divisions of the centromeres
11	»	0,5	» » » » »
7	»	35,0	Polymitosis
15	»	37,0	»
5	72	22,5	»
6	55	45,1	»
2	86	32,1	Weaker aberrations
3	73	24,2	» »
4	—	—	» »
18	52	—	» »
19	57	23,4	» »
20	67	48,0	» »
9	78	54,7	No cytological investigation
17	74	31,0	» » »
22	65	0,9	» » »
23	62	44,6	» » »
24	80	16,9	» » »

Further, especially in plant 11, there were often bicentric chromatids and fragments, and in exceptional cases 2 and 3 bicentric chromatids were found in the same PMC.

The remaining two ♂-sterile plants were characterized by polymitosis, as described above. Two other polymitotic plants, however, produced pollen. The actual state of the case is undoubtedly that there was no polymitotic division in solitary panicles or parts of panicles. In polymitotic plants, thus, external influences of some kind or other must at times prevent a polymitosis from occurring. In three of the polymitotic plants there was a low but significant univalent frequency (see above). In plants 6 and 7 bicentric chromatids with fragments appeared, in plant 6 fairly commonly and in plant 7 rarely. Characteristic of the polymitotic plants is a high ♀-fertility, indicating that this abnormality has no analogy in megasporogenesis.

Of the ♂-fertile plants, six were submitted to cytological examination. In all of these there was some univalent frequency, besides which bicentric chromatids with fragments were observed in five. Statistics showing the univalent frequency are given below, except for plant No. 3. The fixation of this contained so few PMC's at I—M that no statistical treatment was undertaken.

	No. of univalents per PMC						
Plant No.	0	2	4	6	10	14	M
2	23	30	15	1	1	0	1,94
4	29	17	1	1	1	1	1,36
18	25	16	8	0	0	0	1,31
19	42	7	1	0	0	0	0,36
20	35	13	2	0	0	0	0,68

Without doubt the ♂-sterility is conditioned by recessive factors. The meiotic aberrations in the two plants No. 12 and No. 16 may conceivably be governed by the same main factor, since the prophase degeneration of the pollen mother-cells of plant No. 12 may be interpreted as an extreme case of the retarded meiosis found in plant 16. In that case the phenotypical expressions of this main factor should be modified by other factors. The small meiotic disturbances found in the ♂-sterile plants 1, 10 and 25 probably do not stand in any causal relation to their ♂-sterility, as disturbances of the same kind and degree are also present in fertile sibling-plants. No doubt the ♂-sterility in these cases is attributable instead to an abortion of gametes after »normal meiosis».

On these assumptions the following five independent abnormalities of microsporogenesis would be present: retarded meiosis, strong partial asyndesis, gamete abortion after normal meiosis, premature centromere division, and polymitosis. Each of these disturbances may be assumed to be governed by its specific, recessive factor, without effect in the heterozygotic condition. Another reasonable assumption may be that plants homozygous for more than one of the recessive factors are lethal. Of the 1024 combinations that are possible in five-fold heterozygosity, 243 are not homozygous for any recessive factor, 405 are homozygous for one recessive factor, and the remaining 376 are homozygous for more than one recessive. If the last-mentioned category

TABLE 16. *The ♂-fertility of the progenies of Tabor I_1 plants after open pollination.*

Mother plant No.	Type of the mother plant	Percentage of good pollen														
		0	30	35	40	45	50	55	60	65	70	75	80	85	90	95	Mean
6	polymitosis	1					1	1	2		3	3	1		4	9	81,5
7	»						1			1		2		2	5	14	88,6
13	asynapsis	1					1				4	1	2	3	6	6	83,9
14	»		1												2	1	76,3
15	polymitosis				1		1	1	2	2		3	2	3	5	5	78,4
20	fertile	1			1		1	2	1	2	1	2	3			7	76,0
21	asynapsis						1								1		70,0
22	fertile														1		95,0
	Totals	3	1		2		6	4	5	5	8	11	8	8	24	42	80,1

is not realized, the ratio between normal and aberrant plants would thus be 243 : 405, or for 25 individuals 9,4 : 15,6, with a mean error of 2,4. The actual ratio 11 : 14 agrees well with the hypothetical one. Each of the recessive homozygotes would be realized with a frequency of 81/648, which corresponds to a frequency of $3{,}1 \pm 1{,}32$ plants in 25. This condition is also fulfilled, as the five aberrant classes are here represented by 2, 3, 3, 2, and 4 plants. This hypothesis, which presupposes five specific factors, seems to be the simplest, although the present problem may also be explained by the assumption of a smaller number of recessive factors and interaction between these.

In no fewer than 13 of 20 cytologically examined plants a greater or less frequency of bicentric chromatids with fragments was observed. Further, a certain low univalent frequency appeared to be typical of all plants not subject to major disturbances. From this it is evident

that the original plant had been heterozygous for presumably several inversions, which, in view of the invariably low frequency of bridges, were probably small. It can therefore very well be thought that a greater or less number of the recessive factors are inversions, in such a case probably linked with deficiencies.

Progenies were raised from eight I_1 plants after open pollination. The ♂-fertility of these is given in Table 16. Of the total 131 plants, 127 could be classified with regard to their ♂-fertility. Only three were ♂-sterile, while 124 were fertile. One of the sterile plants possessed retarded meiosis, and one had normal syndesis, though the loculi were almost entirely filled with, frequently very large, syncytes. The third ♂-sterile plant had regular meiosis, apart from some degree of univalent frequency. Vegetatively these progenies were composed entirely of vigorous and very vigorous plants.

TABLE 17. *The ♀-fertility of descendants of Tabor and München.*

Plant	I = selfed K = cross pollinated	Number of spikelets with seeds	Number of spikelets without seeds	Spikelets with seeds %
Tabor	I	30	392	7,1
9—4	I	8	500	1,6
München	I	32	1072	2,9
Tabor	K	37	160	18,8
München	K	71	208	25,4

Attempts have been made to raise an I_2 family by self-fertilization of plant 4 from family 9. The seed setting of the plant after self-fertilization was, however, very poor, as can be seen from Table 17. Only eight seeds were obtained and none of these germinated.

The I_1 of München, family 10, comprised 18 plants. Of these, nine were found to be ♂-fertile and three ♂-sterile, while the others could not be classified. Two of the ♂-sterile plants had an abnormally strong chromosome contraction (Figs. 28—35). One of this also showed a rather strong partial asyndesis, as can be seen below:

No. of univalents per PMC	0	2	4	6	8	10	12	M
No. of PMC's	3	12	10	12	10	2	2	5,1

There was also a not inconsiderable syncyte frequency.

The fixation of the third ♂-sterile plant contained no divisions. However, the probability is that the same cytological conditions were also present in this. This abnormally strong chromosome contraction

is in all probability a symptom of a physiological disturbance involving a retarded meiotic rhythm and ultimately an abortion of the pollen-grains. Meiosis was also studied in five fertile and three non-flowering sister-plants. None of these plants exhibited any abnormality whatever. The ratio of fertile to sterile plants is suggestive of a monohybrid segregation.

Families 22 and 23, representing the reciprocal F_1 families between Tabor and München, comprised altogether 33 plants. Pollen samples were obtained from 23, while one plant was found to be ♂-sterile. The ♂-sterile plant was distinguished by a certain amount of univalent frequency, besides which bicentric chromatids with fragments occurred rarely. The univalent frequency was as follows:

No. of univalents per PMC	0	2	4	6	8	10	M
No. of PMC's	18	32	14	5	2	1	2,4

As the Tabor parent had plainly proved to be heterozygous for inversions, it was natural that inversion heterozygotes should also appear in the F_1. The ♂-fertile plants were not cytologically studied. If they had been, it is probable that inversion symptoms in the form of solitary bicentric chromatids and a low univalent frequency would also have been found in a number of the fertile sister-plants.

5. SOME I_1 AND F_1 FAMILIES.

Some, as a rule, small I_1 families from original plants with low self-fertility are collected in Table 18. Families 2 and 5 with respectively Lyons and Liége as sources comprised only one plant each. The Lyons plant was weak, and never flowered. The likewise weak Liége plant, however, flowered and proved to be fertile, yielding 73 % good pollen. The I_1 of Tashkent, family 6, comprised nine plants, which with two exceptions were very feeble. A pollen sample was obtained from one plant, and two plants were found to be ♂-sterile. PMC fixations were obtained from seven plants, including the two ♂-sterile ones. In all cases there was a low univalent frequency, with two univalents in one PMC in about 10—25. One of the sterile plants also showed syndiploidy and syncytes, and one plant of undetermined ♂-fertility had some bicentric chromatids with fragments.

Family 8, which forms the I_1 of Brussels, numbered 17 plants. These were of a vigorous, many-leafed and late type. Nine plants were found to be ♂-fertile, the pollen vitality varying between 75 % and 99 %.

TABLE 18. *Descendants of Lyons, Liége, Tashkent and Brussels.*

Family No.	Origin	Spikelets with seeds %	Number of plants	♂-fertility number of plants		Good pollen %		
				fertile	sterile	Min.	Max.	Mean
2	Lyons	4,9	1	—	—	—	—	—
5	Liége	0,4	1	1	0	—	—	73
6	Tashkent	2,8	9	1	2	—	—	97
8	Brussels	5,1	17	9	0	75	99	82,7

Table 19 includes the I_1 families and the reciprocal F_1 families having Brunn and Nancy as sources. To the eye Brunn showed good self-fertility, having 55,1 % spikelets with a seed. Of the 120 seeds sown, however, only one germinated. This plant was vigorous and ♂-fertile, with 57 % good pollen. The original plant from Nancy was very self-sterile. The I_1 family therefore came to comprise only two plants, which were vigorous, many-leafed and few-strawed. The two F_1 families comprised altogether 16 plants. These resembled the I_1

TABLE 19. *Descendants of Brunn and Nancy.*

Family	Origin	Spikelets with seeds % after		Number of plants	♂-fertility number of plants		Good pollen %		
		selfing	cross pollination		fertile	sterile	Min.	Max.	Mean
7	Brunn	55,1		1	1	0	—	—	57
20	»		82,2	8	4	0	78	92	84
3	Nancy	1,5		2	1	0	—	—	95
21	»		27,1	8	2	0	80	95	87,5

plants in being a vigorous, many-leafed and exceedingly late type. Pollen samples were obtained from six plants, the pollen vitality of which was between 78 % and 95 %. No cytological examinations were undertaken on this material.

XI. ABSOLUTE STERILITY.

Absolute ♂-sterility with non-bursting anthers as an external symptom is not an uncommon phenomenon in nature and has often been observed in experiments. The cause of absolute ♂-sterility may be of the most varying kinds. The sterility phenomenon as a whole

can be classified into two main groups, haplontic and diplontic sterility (MÜNTZING, 1930). Haplontic sterility is characterized by absolute or partial lethality in the haplophase, caused by the latter's genotypic constitution. Absolute or almost absolute lethality in the haplophase is a frequently recurring cause of absolute ♂-sterility. Sterility of this nature is often caused by numerical or structural hybridity, as in real haploids, in autotriploids, and especially in species hybrids. As a rule, it is then a question of a more or less complete asynapsis with random distribution of the unpaired chromosomes between the daughter nuclei during meiosis, which results in haplonts with unbalanced chromosome sets. Asynapsis governed not by numerical or structural hybridity but by genic constitution leads in the same way to haplonts with unbalanced chromosome sets. Absolute ♂-sterility from this cause has here been described in *Alopecurus myosuroides* and was previously known in several plants, e. g. *Zea mays* (BEADLE, 1930), *Viola Orphanides* (CLAUSEN, 1930), *Hevea* (RAMAER, 1935), etc.

In cases of stickiness as well, such as described here for *A. myosuroides* and earlier by BEADLE (1932 b) for maize, the sterility is apparently to be regarded as haplontic, as the pollen-grains resulting from this type of meiosis have an extremely unbalanced chromosome set. The premature centromere division, which brings about random chromosome distribution in II—A, must likewise lead to unbalanced chromosome sets, and consequently the sterility in plants with this abnormality must fall within the boundaries of haplontic sterility.

When polymitosis occurs, the sterility is also often absolute, that is to say, it is absolute in all flowers within which polymitotic division takes place. The random chromosome distribution in polymitosis leads to pollen-grains that are nullisomic for a greater or less number of chromosomes. Such pollen-grains, of course, are *a priori* to be considered as lethal in a diploid plant. It is accordingly quite clear that sterility caused by polymitosis is haplontic. On the other hand, it is open to question whether the polymitotic division is diplontically or haplontically initiated. Plants subject to polymitosis are homozygous for a recessive factor. This may be conceived as exercising its primary action within the diplont, an action that by some sort of hormonal induction initiates the polymitotic division in the haplont. On the other hand, it is conceivable — and may be more probable — that the recessive factor acts directly within the haplont.

When absolute sterility has the character of a general degeneration of the pollen-grains after a normal meiosis or after a meiosis with only

minor disturbances, the question of haplontic — or diplontic — sterility cannot be decided. Absolute sterility of this nature has been found within several *Alopecurus* families. In maize BEADLE (1932 a) has found no fewer than 16 non-allelic recessives that lead to pollen degeneration after normal meiosis. Absolute ♂-sterility after normal meiosis has been further described in, e. g., *Hevea* (RAMAER, 1935), *Oenothera organensis* (EMERSON, 1938), and *Hebe* (FRANKEL, 1940). The direct cause of the pollen lethality in such cases may be diplontic, e. g. degeneration of the tapetum, or disturbances in the exchange of nutriment between soma and pollen-grains, or haplontic, directly conditioned by a lethal haplontic constitution. In all probability both types are realized. A remarkable case of this category is the maternally inherited ♂-sterility that RHOADES (1933) has found in maize. Here belongs also the classical case of plasmatic sterility in flax (GAIRDNER, 1929).

Haplontic, absolute ♂-sterility in *A. myosuroides* resulting from absolute asynapsis, stickiness and premature centromere division has also been accompanied by absolute or nearly absolute ♀-sterility. The probability is that the ♀-sterility in these cases is due to the same factors as the ♂-sterility. In maize, too, the ♀-fertility is greatly reduced in asynaptic and sticky plants. The polymitotic plants, however, do not display any sign of reduced ♀-fertility. In cases of absolute ♂-sterility with partial asynapsis and normal meiosis the ♀-fertility is also strongly reduced as a rule, but there are also plants that show no considerable reduction in their seed production.

An absolute ♂-sterility of unquestionably diplontic nature is present in *A. myosuroides* as well as *Lathyrus* (UPCOTT, 1936; FABERGÉ, 1937) in association with retarded meiosis. Here it is evident that the diplontic constitution is a direct cause of the sterility, since not infrequently meiosis already ceases at I—M or even during prophase.

As in most cases of haplontic sterility, not only ♂-sterility but also absolute or almost absolute ♀-sterility attends retarded meiosis in *A. myosuroides*, whereas in *Lathyrus* the corresponding phenomenon is attended by full ♀-fertility.

Diplontic sterility, defined by MÜNTZING (1930) as »*absolute or partial inability to produce progeny in a sexual way caused by an absolute or partial lethality of the diplophase*», does not cover the hypothetical cases adduced above, as the pollen-grains degenerate after meiosis and there is reason to assume that their genetic constitution is not lethal in itself but that the pollen lethality has its origin in disturb-

ances of the physiological *diplont—haplont* interaction. For the sake of completeness, therefore, MÜNTZING's definition ought to be supplemented to this effect: . . . *or by lethal influences of the diplophase on the haplophase.* It would thus be clearly laid down that diplontic sterility may consist in lethality at all stages of development but also in an unfavourable influence of the diplont on (or interaction with) the still dependent haplont.

In *A. myosuroides* diplontic sterility occurs of several different types, especially after inbreeding. Sterility of this type has been discussed above in connection with retarded meiosis, in addition to which it has been suggested that sterility following normal meiosis may be of diplontic nature. A noteworthy category showing diplontic sterility is afforded by the small and feeble plants which appear after inbreeding and which do not produce panicles or whose panicles are malformed and stunted. Undoubtedly recessive segregating products are concerned here. Another type of diplontically sterile plants among the cultivations is vegetatively luxuriant but does not flower. This diplontic sterility is probably facultative, however, and is no doubt associated with ecotypes selectioned under different light-climate conditions.

An all-round discussion of diplontic sterility is to be found in MÜNTZING's paper of 1930. Here, reference will only be made to the one-sided diplontic sterility, evidently often of non-Mendelian character (CORRENS, 1928), which is found within gynodioecious and androdioecious species. Similar gene-controlled phenomena have also been found in unisexual maize (JONES, 1934).

XII. PARTIAL STERILITY.

In the foregoing account plants which have shed pollen have been denoted as fertile. However, the data submitted have at the same time shown that the majority of these plants possessed a pollen that was characterized by a higher or lower percentage of dead grains. The investigation embraces altogether 632 pollen-yielding plants of different categories. Of these, only 109 plants or 17 % had between 95 % and 100 % good pollen, while the percentage of good pollen in the rest varied between 27 and 95. On an average the 632 ♂-fertile plants had 78,6 % good pollen, or, viewed from the opposite standpoint, their pollen lethality averaged 21,4 %. The degree of sterility was of approximately the same order both within the F_1 families between plants of different geographical origin and within inbred families. This can

TABLE 20. *Comparison of ♂-fertility within successive inbred families.*

Origin	Generation	♂-sterile plants	Percentage of good pollen															Number of partially ♂-fertile plants	Mean $I_3 - I_1$
			27,5	32,5	37,5	42,5	47,5	52,5	57,5	62,5	67,5	72,5	77,5	82,5	87,5	92,5	97,5	Mean	
0—4	I_1								*1*	2			1				1	71,0	5	
	I_2				1		4	2	*2*	1	3	5	3	4	2			67,3	27	+ 4,1
	I_3					2		1			1	2	1			2	3	75,1	12	
Rennes	I_1	2				1			*1*	5		4	2	1				66,7	14	
	I_2		1							1	2		5	2	3	2		75,9	16	+ 20,8
	I_3														2			87,5	2	
Rouen	I_1							1	1			1			1	1	*1*	75,8	6	
	I_2	6					1			1			*1*		3			74,5	6	+ 0,7
	I_3	3				1					1	2	2	2	1	1	1	76,5	11	
Jena	I_1				1	1			1		1	2	3	3		4	2	77,2	18	
	I_2	3										1	2	*5*	5	3		84,3	16	+ 11,1
	I_3	6								1					4	3	2	88,6	10	
Paris	I_1					1					1	1	2	1	*1*	1	9	87,0	17	
	I_2							2			1	1	5	3	7	4	2	81,6	25	− 3,2
	I_3					2		1			1	2	1			2	3	75,1	12	
Totals	I_1	2			1	3		1	4	7	2	8	8	5	2	6	13	77,17	60	
	I_2	9	1		1		5	4	2	3	6	7	16	14	20	9	2	76,67	90	+ 2,5
	I_3	8				5		2		1	3	6	4	2	7	8	9	79,24	51	

be seen, for instance, from Table 3, according to which 70 F_1 plants out of four different crosses had on the average 83,1 % good pollen and 88 I_1 plants out of eight different I_1 families averaged 77,0 % good pollen.

The percentage of good pollen for the successive inbred generations I_1, I_2 and I_3 is summarized in Table 20, in which the class to which the original plant for the next generation belongs is printed in italics. The sterility conditions within the different families appear to be approximately the same, with averages between 70 % and 80 %. The changes in pollen vitality from generation to generation are small and uncertain. For all the I_1 families the mean is 77,17 % and for all the I_2 families it is 76,67 %. From the I_2 to the I_3 a certain increase in the mean has occurred, this being 79,24 % in the I_3. Within four of the five sources the I_3 thus had better pollen fertility than the I_1.

The ♀-fertility, even after cross-pollination, is likewise reduced. Some data on this point are given in Table 2. The seed setting following cross-pollination varies for the 10 plants contained in the table between a maximum value of 82,2 % and a minimum of 18,5 %, while the average amounts to 52,7 %. Hence the conclusion suggests itself that *A. myosuroides* is characterized by partial male as well as female sterility.

Partial sterility, like absolute sterility, may be haplontic or diplontic. Partial haplontic sterility may be due to the same causes as a corresponding absolute sterility, namely numerical and structural hybridity, genic meiotic disturbances, and specific gamete-lethal genes. If the sterility attending such disturbances is only partial, it has *a priori* to be assumed that the disturbances are of a milder degree than when the sterility is absolute.

Examples of numerical hybridity, which may give rise to partial sterility, are monosomy and trisomy. Especially in the former case it is to be expected that the nullisomic gametes that arise will be lethal in a diploid organism. However, in the present cases, numerical hybridity as a cause of sterility can be entirely left out of account, as a plant with a deviating chromosome number was never observed.

Partial sterility caused by structural hybridity has been found in a large number of plants. Attention has in this connection been especially directed to reciprocal translocations. Even before the cytological symptoms and genetical consequences of these translocations had been more closely investigated, BELLING (1925) stated that the semi-sterility he had described earlier in *Stizolobium* (BELLING, 1914), and then interpreted on a factorial basis, agrees with what would be expected if a reciprocal translocation had occurred. Later, translocation sterility has

been studied especially in *Pisum* (HÅKANSSON, 1929; SANSOME, 1929; E. NILSSON, 1936) and in *Zea* by BRINK (1927) and others. These investigations have shown that individuals which are heterozygous for a reciprocal translocation (segmental interchange) in typical cases possess a quadrivalent and 50 % pollen lethality. This implies that that half part of the pollen-grains which come to contain one normal chromosome plus one translocation chromosome are not viable. However, it has been found that the quadrivalent frequency as well as the pollen lethality may vary in translocation heterozygotes. Respecting pollen lethality BRINK and COOPER (1931), for instance, found that 198 semi-sterile plants from »semi-sterile-1» in maize, which almost always possesses one ring-quadrivalent per PMC, had on the average 50,25 % pollen lethality. As between the plants, however, the frequency of poor pollen ranged from 39 % to 67 %. In another case of translocation heterozygosity in maize the pollen lethality always proved to be lower than 50 % (CLARKE and ANDERSON, 1935), and in six plants was respectively 19, 26, 43, 44, 45 and 47 per cent. Finally, BURNHAM (1930) found likewise in maize an average sterility of only 25 % in connection with segmental interchange, which makes it clear that only one of the recombination products was lethal. The same condition has also been found by ANDERSON (1935) in maize, and in this case the sterility fell even below 25 %. It has thus been elucidated that structural hybridity in the form of segmental interchange can produce partial sterility of varying degree, depending on the frequency in which the recombination gametes are formed and the degree of lethality possessed by the reduplications and deficiencies, which in its turn depends to an essential degree on the size of the interchanged segments. Segmental interchange may therefore be conceived to be capable of causing a partial sterility that corresponds to a percentage of good pollen lying between 40 and 90 %, such as in the present material (see Table 20). However, any hypothesis ascribing partial sterility in *A. myosuroides* to segmental interchange would have gained in strength if there had been a larger accumulation of plants with about 50 % and about 75 % good pollen. A development of such modes cannot, however, be considered as unconditionally necessary. If there are different segmental interchanges in different families, recombination gametes may be formed in different frequency. Both of these, or only one, may be absolutely or partially lethal in different translocations. On these lines the picture of a continuous variation can obviously be conceived to arise.

In the typical case of segmental interchange, however, there is a

quadrivalent, as a rule ring-shaped, in at all events the majority of PMC's at I—M. In not a single *A. myosuroides*, however, was any quadrivalent observed. The question is then to what extent quadrivalent frequency has been found to vary in translocation heterozygotes and to what degree of probability it can be assumed to be entirely suppressed.

That the quadrivalent frequency is by no means always 100 % is shown for instance by the above-cited investigation of maize by CLARKE and ANDERSON (1935). In this case there were only bivalents in most of the PMC's. A chain-shaped quadrivalent appeared, however, in 31 % of 1500 PMC's. It is obvious that this case does not represent any minimum value. It is quite conceivable that qaudrivalents occur in such low frequency at times as to make it difficult to find any quadrivalent at all at the cytological examination. It may also be assumed that translocations can occur which do not find expression in quadrivalent formation. In that case the interchanged segments are probably very small. In spite of their small size it is manifestly possible for them to exercise an influence on gamete vitality. Still, it would be rather peculiar if the partial sterility in *A. myosuroides* were mainly governed by such small cytologically undetectable segmental interchanges. Hence the conclusion presents itself that structural hybridity in the form of segmental interchange cannot play any notable part in the partial sterility found in *A. myosuroides*.

Heterozygosity for inversions may also lead to partial sterility. In cases of segmental interchange it is obvious that the sterility arises independently of whether any cytological complication — quadrivalent formation — is present or not. When inversions are present, however, the sterility is directly connected with the cytological complication, here depending on bicentric chromatids with fragments, unless the inversion is combined with some other structural alteration, e. g. deficiency, which is quite conceivable. In plants that are heterozygous for inversions (disregarding species hybrids) the frequency of bicentric chromatids is seldom high. Sterility produced by them cannot, therefore, be expected to be especially great. Bicentric chromatids have been found in low frequency in a great many partially sterile *Alopecurus* plants. However, it is inconceivable that inversion heterozygosity can be the main cause of the partial sterility, but it may very well be an accessory factor, though of relatively limited significance.

Another category of structural aberrations that are often responsible for gametic lethality consists of deficiencies. In maize, for instance, a

correlation between semi-sterility and deficiencies has been found in two cases (STADLER, 1932; BURNHAM, 1941). Practically speaking, however, there is no possibility of cytologically determining the presence of deficiencies in other than especially favourable instances. In *Drosophila*, the salivary-gland chromosomes of which lend themselves to the discovery of even small structural changes, deficiencies having a lethal action have proved to be numerous. There is no possibility of judging to what extent deficiencies contribute to the partial sterility in *A. myosuroides*.

These considerations make it clear that, as a main cause of the partial sterility in *A. myosuroides*, structural heterozygosity only seems to be possible in the form of deficiencies.

Gene-controlled meiotic disturbances of a rather weak type certainly play some part in bringing about partial sterility. The meiotic aberration that demands first consideration is partial asynapsis. It has already been shown that partial asynapsis of all degrees occurs within the species. Even many partially fertile plants exhibit weak partial asynapsis. If this asynapsis is gene-controlled, there must be a direct correlation between degree of asyndesis and gametic lethality, since no other gametes would have a lethal constitution than some of those which are derived from PMC's with univalents. As partially sterile plants seldom had univalents in more than one PMC in 10, the contribution of partial asyndesis to pollen-sterility cannot be so very considerable.

A low univalent frequency need not, however, of necessity be gene-controlled. It may be an expression of small structural differences, and in such cases the sterility of the respective plant may obviously be far greater than the univalent frequency indicates. Still, it seems probable that weak partial asynapsis, at least in the majority of cases, is gene-controlled, since the transition to stronger asynapsis, which is undoubtedly gene-controlled, is very gradual.

The chief cause of the partial sterility, therefore, is scarcely to be sought in gene-controlled meiotic disturbances.

If the partial sterility is haplontic, only one possibility now remains, viz. that gamete-lethal genes are present. Considering the wide range of variation and the small selection effect, rather many such genes must in that case be assumed. A fairly simple pattern, however, may illustrate this gene-controlled partial sterility rather well. Let us assume a plant that is heterozygous for, e. g., the three genes S_1, S_2, and S_3. With regard

to these genes the plant produces the following kinds of gametes: $S_1\ S_2\ S_3$; $S_1\ S_2\ s_3$; $S_1\ s_2\ S_3$; $s_1\ S_2\ S_3$; $S_1\ s_2\ s_3$; $s_1\ S_2\ s_3$; $s_1\ s_2\ S_3$; $s_1\ s_2\ s_3$.

Assuming the three last-mentioned combinations, i. e. $s_1\ S_2\ s_3$, $s_1\ s_2\ S_3$ and $s_1\ s_2\ s_3$, to be absolutely pollen-lethal and the others absolutely vital, the plant in question should have 62,5 % good pollen. Should all the kinds of gametes be viable on the ♀-side, the progeny after self-fertilization would be composed of plants with different percentages of good pollen in the following frequencies.

% good pollen	100	75	62,5	50	25
No. of plants	19	9	5	6	1

The average good pollen for the progeny would be 80,3 %. If there is a contemporaneous influence from other factors that produce low sterility, such as inversions, gene-controlled weak asynapsis, and diplontic effect (see below), the frequency of fully fertile plants would drop, just as the average would also be depressed. It seems probable that the main cause of the partial sterility is to be sought in genes with gamete-lethal action. Probably their number is greater than that given in the above diagrammatic picture. Sublethal categories of gametes probably also occur alongside the fully vital and the absolutely lethal, whereby the continuous variation becomes still more pronounced. It is scarcely probable that these genes are always really intragenic changes in comparison with the normal gene. Most likely small structural alterations having the effect indicated are also present. On the strength of the results obtained in research-work on *Drosophila* especially minor deficiencies are to be expected. It would therefore certainly be more correct to speak of Mendelian factors and to include in this concept true genes as well as cytologically undetectable structural changes.

The possibility of the partial sterility being diplontic remains, however, to be considered. MÜNTZING and PRAKKEN (1941) have found that 50 % of 610 rye plants have a diminished ♂-fertility. In 6 % of the plants there were also distinct meiotic aberrations of various kinds, and the authors consider that structural differences are the principal cause of the pollen sterility. However, it is assumed that a considerable part of the sterility is diplontic. The authors support themselves here, among other things, on the fact that the fertility as well as the frequency of cytological disturbances can vary in the same plant. This variation, however, may in part be interpreted as a consequence of sampling

errors and modificative influences. In *Solanum tuberosum*, for instance, STOW (1927) has found that meiosis proceeds normally under low temperature, while univalents make their appearance under higher temperature and sterile pollen is formed. Another argument advanced by the authors is that different varieties of rye show different sterility without any differences having appeared in the frequency of meiotic disturbances. This may presumably depend on the presence of different gamete-lethal Mendelian factors in different varieties, for it seems as though a good portion of the partial sterility in rye as well as in *A. myosuroides* is attributable to such factors. This does not exclude the possibility that a certain measure of diplontic sterility exists in the two species. If diplontic sterility were of more essential importance in *A. myosuroides*, a more gradual transition between completely empty and completely filled grains ought, however, to be expected. The diplontic influences ought not to act so precisely in one direction or the other. The fact is, however, that the difference between good and poor grains is almost always perfectly sharp. Only in exceptional cases has any degree of continuous variation been observed.

There are undoubtedly sterility causes of the same nature on the ♀-side as on the ♂-side. A general observation, however, is that the lethality of definite sublethal kinds of gametes (e. g. bisomic) is less in the embryo-sacs than in the pollen-grains.

The fact that in spite of this the percentage of seed setting in *A. myosuroides* is lower than the percentage of good pollen is not of a nature to cause surprise. Many apparently good pollen-grains are certainly non-functional, and therefore the percentage of good pollen is probably an overhigh expression for the pollen vitality. The diminished seed setting is further dependent on several co-acting factors, viz. (1) possibly existing deficient pollination, (2) gamete lethality, (3) zygote and embryo lethality.

MÜNTZING's view that the allogamous species are characterized by reduced fertility (MÜNTZING, 1938, 1939) is fully confirmed by the present investigation. This state of things must be regarded as a very important feature in the biology of the allogamous plants. Partial sterility is characteristic of the spontaneous populations. It seems, in any case in *A. myosuroides*, for the most part to be haplontic and controlled by Mendelian factors. These factors may be true genes or structural alterations without cytological symptoms.

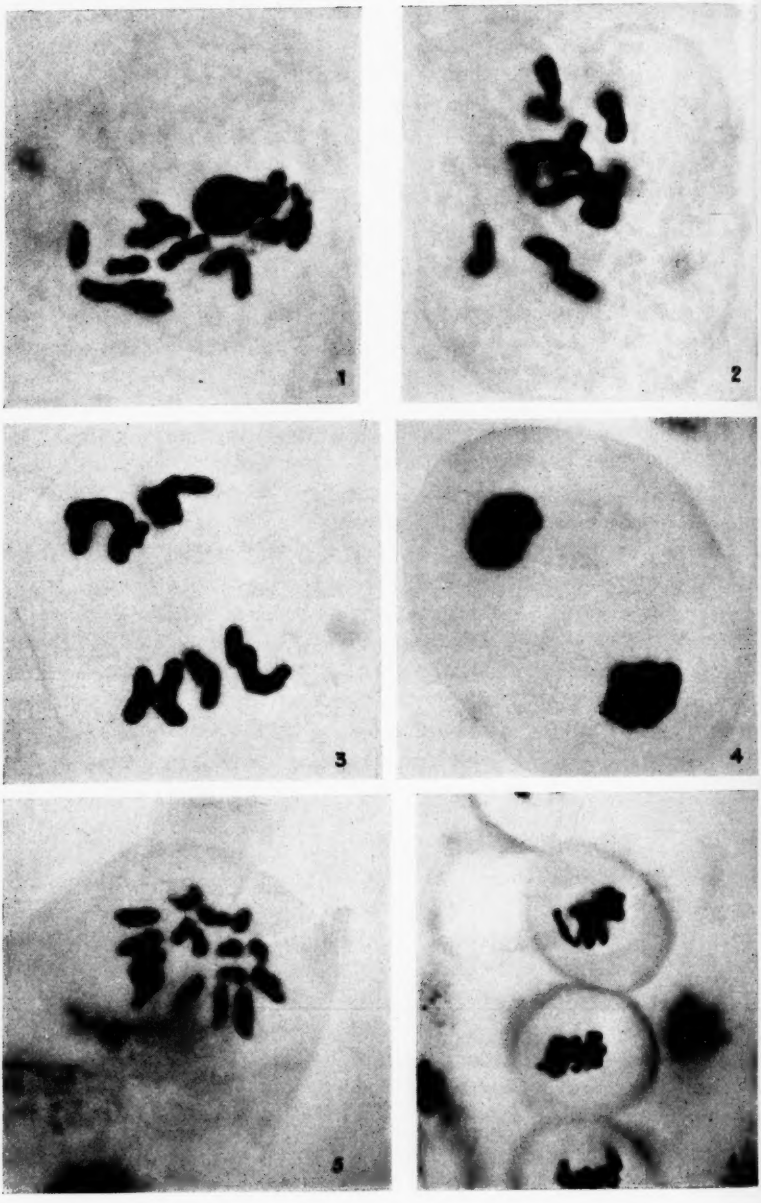
That there also occur such factors as are not gamete-lethal but vitality-reducing in the homozygous condition is shown by the de-

pression resulting from inbreeding, such as this phenomenon has been explained by JONES (1917). Within the populations, however, there are also — in any case in *A. myosuroides* and rye (PRAKKEN, unpubl.) — Mendelian factors which in the homozygous condition lead to a breakdown of the meiotic mechanism, and therefore the inbreeding phenomena cannot be altogether explained on Mendelian grounds (MÜNTZING, 1943).

XIII. DISCUSSION.

Alopecurus myosuroides has been found to possess all the properties characteristic of an allogamous species. Enforced self-fertilization is attended by reduced seed setting of varying degree in different plants. Different inbred families may be very unlike in habit. Some families are on an average fairly vigorous, others present a picture of a considerable vitality depression. Non-flowering plants occur in great number. They belong to two main types, one represented by vegetatively very feeble, sublethal plants, the other by vegetatively luxuriant but despite this non-flowering or only sparingly flowering plants. Quite naturally, this latter type directs thoughts to the presence of a photoperiodic differentiation within the species. *A. myosuroides* can be denoted as a Central European species. In Sweden it occurs mostly within the adventitious flora. The locality in which the experimental material has been cultivated thus lies considerably to the north of the range of the species, which is characterized by a relatively short day. It is possible that special short-day forms have differentiated out within the species. When a short-day form is transferred to a light climate with a relatively long day, the usual consequence is a protracted vegetative development without fructification, as is the case with the diplontically sterile plants of the last-mentioned main type. The contemporaneous occurrence of day-neutral forms which preserve normal relations between vegetative and fructificative phases during cultivation under relatively long-day conditions is not surprising.

Both inbred and cross *Alopecurus* families showed a reduced male and female fertility. This decline in fertility manifested itself, firstly, in the partial pollen lethality and reduced seed setting of some plants, secondly, in the complete ♂-sterility and at the same time often complete ♀-sterility of some plants. Of the total number of plants examined, 977, only 109 or 11,2 % had perfect pollen, 523 or 53,5 % had partially sterile pollen with the percentage of good pollen between 27 and 95.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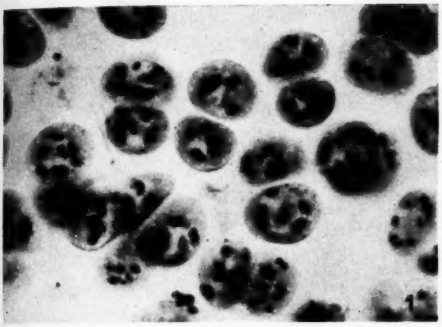

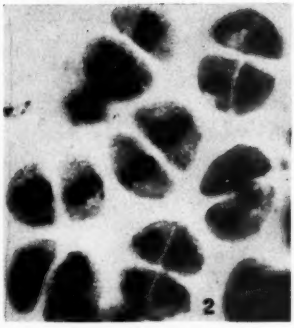

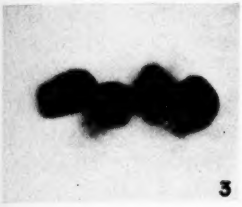

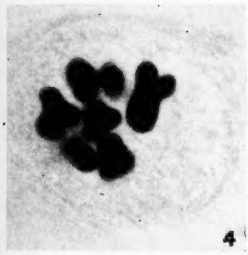

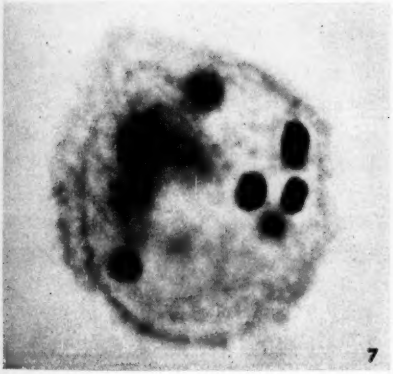

Completely ♂-sterile plants occurred to a number of 86, corresponding to 8,8 % of the total number. The remaining 259 plants could not be classified in regard to fertility owing to a great many of them dying before flowering and many failing to flower, as previously stated. There was, however, a distinct difference in this respect between inbred families on one hand and cross families and families constituted after open pollination on the other hand. After crossing and open pollination only four absolutely ♂-sterile plants made their appearance, while the bulk of the ♂-sterile plants appeared in inbred families. The frequency of ♂-sterile plants was thus very considerably raised as a result of inbreeding. This is explained by the fact that the ♂-sterile plants were homozygous for relatively rare recessive genes within the populations. As a rule, the factorial base did not seem to be complicated. Several cases were encountered where the frequencies obtained for ♂-sterile plants argued strongly in favour of a monohybrid segregation. Absolute ♂-sterility, however, is not a univocal phenomenon. It is chiefly a question of sterility of haplontic nature, caused by gene-conditioned meiotic and microsporogenetic disturbances. The following disturbances of this type have been observed: absolute and partial asynapsis, stickiness, premature centromere division, retarded meiosis, and polymitosis. However, a number of cases of absolute ♂-sterility exhibit no disturbances whatever, either of the meiosis or of the microsporogenesis, but the apparently normal, young pollen-grains abort. This form of absolute ♂-sterility may be haplontic, caused by specific genes with gamete-lethal action, or diplontic and caused by disturbed relations between pollen and somatic tissue.

Except for some cases of polymitosis and partial asynapsis the absolute form of ♂-sterility was accompanied by absolute ♀-sterility or by very strong partial ♀-sterility.

It is worthy of note that the majority of gene-controlled meiotic disturbances met with here have also been described in maize, especially by BEADLE (1930, 1931, 1932 a, 1932 b, 1933 a, 1933 b) and also seem to occur in rye (PRAKKEN, unpubl.). These disturbances are probably to be regarded as common aberrations, in any case in allogamous plants. More or less complete asynapsis of a genic nature has already been demonstrated in a fairly large number of plants and has been discussed in detail by PRAKKEN (1943).

The partial form of sterility, on the other hand, does not seem to be preceded as a rule by any meiotic disturbances, whether of genic or structural character. Thus, no symptoms whatever of segmental

interchange were ever observed within the species. The only meiotic aberrations observed in partially sterile plants consisted of inversion symptoms and a low univalent frequency. Plants exhibiting a bicentric chromatid with fragment in solitary cells were rather common. In no case, however, was there found a higher frequency of bridges than one in 10 PMC's. Inversion heterozygosity, therefore, can scarcely be the main cause of the partial sterility. The low univalent frequency present in solitary partially sterile plants may be a symptom of heterozygosity for deficiency or other structural changes. However, in view of the completely continuous transition from the weakest asynapsis to strong and undoubtedly gene-conditioned asynapsis, it would seem probable that weak asynapsis is also gene-controlled, at any rate in some cases. Further, it must not be ignored that asynapsis may be produced by external conditions, as was shown by STOW (1927), STRAUB (1937) and others.

In rye populations MÜNTZING and PRAKKEN (1941) have found that partial sterility occurs in 50 % of the plants and meiotic aberrations in 6 %. They assume that a considerable part of the partial sterility is diplontic. In the case of *A. myosuroides* diplontic sterility seems less probable, among other reasons because transitions between good and poor pollen hardly ever occur, the two categories being sharply distinct. The partial sterility in *A. myosuroides* is therefore probably of haplontic nature and controlled by Mendelian factors. Whether these factors *per se* are true genes or structural aberrations without cytological effect must be left open. The whole picture presented by partial sterility can be explained by the assumption of a number of different recessive factors with absolutely lethal or sublethal effect on the gametes.

The view advanced by MÜNTZING (1938, 1939) that the allogamous species are characterized by reduced fertility and especially by reduced pollen vitality is entirely supported by the conditions found in *A. myosuroides*. These conditions are no doubt general, to which conception, indeed, the facts adduced by MÜNTZING (1939) point. There are however exceptions. For instance, in the practically speaking absolutely self-sterile species *Betula verrucosa* and *Betula pubescens* the pollen is consistently perfect (JOHNSSON, 1940 b and unpubl.).

A point of great interest is that not a single numerical aberrant was met with in the whole of the material examined. However, in view of the minor meiotic disturbances that were at times found in partially fertile plants, there are grounds for thinking that gametes with aberrant

chromosome numbers were formed. The fact that no such gamete was found to function and to give rise to plants with aberrant chromosome numbers is doubtless to be viewed against the background that a genotypic balance is apparently demanded for the gametes to become vital and functional. The cause of the absence of plants bearing aberrant chromosome numbers is thus probably to be sought in elimination of gametes with aberrant chromosome numbers. As a matter of fact, a frequently observed phenomenon in diploid plants is that individuals having aberrant numbers do not occur in expected frequencies.

A point of still greater interest is that structural aberrants were uncommon and that the important category *segmental interchange* was entirely absent. The only structural deviations observed were inversions, and in view of the invariably low frequency of bicentric chromatids it is probable that the inverted segments were small. The frequency of structural changes and their nature are evidently very dissimilar in different species. A very high frequency of structural aberrations was thus found by GEITLER (1937, 1938) in *Paris quadrifolia*. For instance, 40 plants examined from two adjacent populations were all found to be heterozygous for inversions and showed inversion bridges in $1{,}2$—$12{,}3$ % of the pollen mother-cells. The dominant structural alteration was thus here, as in *A. myosuroides*, inversions, and in both cases these appeared mainly to consist of small segments. Their frequency is, however, substantially higher in *Paris* than in *Alopecurus*.

An allogamous species with segmental interchange as the chief source of structural differences is evidently to be found in *Campanula persicifolia*. Here, among 17 population plants taken at random DARLINGTON and GAIRDNER (1938) found three that were heterozygous for a segmental interchange and one that was heterozygous for two reciprocal translocations. In rye, inversions and segmental interchange seem to be about equally common. For instance, among 167 plants MÜNTZING and PRAKKEN (1941) found five inversion heterozygotes and six plants that were heterozygous for a segmental interchange. In the autogamous species *Galeopsis Tetrahit*, too, structural differences appear to occur very often (MÜNTZING, 1938).

The progeny of crosses between plants with different geographical origin did not exhibit any other peculiarities than partial sterility of approximately the same order as that of the inbred families. No other cytological complications than rare bicentric chromatids and a low univalent frequency in single plants were observed. The number of crosses

carried out was small, however, being only five combinations comprising ten plants. If major structural differences were more general between geographical races within the species, however, some of these crosses ought to have shown clear symptoms of structural hybridity. Gross structural differences between geographical races of the same species do not seem to be at all a common phenomenon. In *Crepis foetida* BABCOCK and CAVE (1938) were thus unable to observe any meiotic disturbances within the F_1 families between nine different geographical races. Nor in the prototype of intraspecific structural differentiation, *Datura stramonium*, are structural differences common, as according to BLAKESLEE and collaborators (1937) 583 races are distributed over only five primary types.

SUMMARY.

(1) A cytogenetical study is submitted of *Alopecurus myosuroides*, based mainly on studies of inbred progenies and cross progenies from plants of different geographical origin. Attention is especially directed to the fertility conditions and cytological aberrations.

(2) The somatic idiogram and normal meiosis of this diploid species are discussed. The seven chromosome pairs, which are of different length, have median or submedian centromeres, and one pair is characterized by a secondary constriction. The chiasmata are incompletely terminalized.

(3) Meiosis of tetraploid plants produced by colchicine treatment shows approximately half the chromosomes associated in quadrivalents.

(4) *A. myosuroides* behaves as a typical allogamous species, showing reduced seed setting after enforced self-fertilization and considerable morphological variation between different progenies.

(5) Within the F_1 families between plants of different origin no cytological aberrations worth mentioning have been found.

(6) Within several inbred families different cytological disturbances have appeared. These are described as absolute and partial asyndesis, premature centromere division, stickiness, hypercontraction, retarded meiosis, polymitosis, and syncyte formation.

(7) The above-mentioned aberrations have almost invariably been associated with absolute ♂-sterility and mostly also with absolute or almost absolute ♀-sterility. Plants with these abnormalities are homozygous for recessive factors. The factorial background is not very complicated, in several cases monohybrid segregations have been found to occur.

(8) Most of the fertile plants are characterized by partial ♂-sterility. The pollen lethality varies greatly, the proportion of good pollen ranging from 27 % up to almost 100 %. The variation seems to be continuous without any clear modes. This partial sterility is not as a rule connected with any meiotic aberrations.

(9) Various elucidative propositions respecting the partial sterility are discussed. The conclusion is arrived at that partial sterility is mainly haplontic and conditioned by Mendelian factors having a gamete-lethal action. These factors may be true genes or structural aberrations without cytological effect.

(10) The importance of partial sterility as a characteristic of allogamous species is stressed, in addition to which the general occurrence of gene-controlled meiotic aberrations and their significance are discussed.

(11) The absence of numerical aberrants and cytologically detectable reciprocal translocations is pointed out, and the occurrence of specific differences in the frequency and nature of the structural aberrations is discussed.

EXPLANATION OF PLATES I AND II.

Plate I.

Figs. 1—4. Absolute asynapsis in a *A. myosuroides* plant. No. 35—7. — Fig. 1. Diakinesis. — Fig. 2. I—M, cf. Fig. 11 (p. 486). — Fig. 3. I—A, cf. Fig. 12 (p. 486). — Fig. 4. Interphase. — Fig. 5. I—A in polar view, showing precocious centromere division, plant No. 9—11. — Fig. 6. PMC's with rounded outlines in I—M, indicating retardation in plant No. 9—8, showing precocious centromere division. — Figs. 1—5 × 3000. Fig. 6 × 750.

Plate II.

Fig. 1. At second prophase retarded meiosis, aceto-carmine squeeze preparation, plant No. 36—5. × 900. — Fig. 2. Normal second divisions from the same plant. × 900. — Fig. 3. Retarded I—M in side view, plant No. 4—1, cf. Fig. 23 (p. 495). × 3000. — Fig. 4. Retarded I—M, polar view, cf. Fig. 24 (p. 495). × 3000. — Fig. 5. PMC's with meiosis retarded at second division, plant No. 9—1 b. × 1000. — Fig. 6. Polymitotic metaphase, plant No. 9—6. × 3000. — Fig. 7. Retarded meiosis at I—A, plant No. 9—1 b. × 3000. — Fig. 8. Retarded meiosis at II—A, plant No. 9—1 b. × 3000.

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INVESTIGATIONS ON DIPLOID, TRIPLOID AND TETRAPLOID LUCERNE

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IN the course of breeding work on lucerne Dr. FREDRIK NILSSON, Manager at the time of the Hay Plant Department of the Swedish Seed Association, produced a number of polyploid plants of lucerne by colchicine treatment in the year 1940. On the progeny of these, propagated from seeds and cuttings, a number of investigations were carried out the following year, the results being published in »Sveriges Utsädesförenings Tidskrift» (NILSSON and ANDERSSON, 1941). Further investigations directed to certain morphological characters have been conducted during the years 1942 and 1943. The chemical composition of the plants has also been the subject of study, and, finally, a cytological treatment of the material has been commenced.

According to SENN (1938), the basic chromosome number of the genus *Medicago* is 8. Of 36 species examined within this genus, 30 have the somatic chromosome number 16. The other six species, among which *M. sativa* L. and *M. falcata* L. are noticed, have the somatic number 32 and are therefore to be regarded as tetraploids. In the investigations reported here plants of *M. sativa* and *M. sativa* × *M. falcata* have been produced with the chromosome numbers 48 and 64, and hence these are to be regarded as hexa- and octo-ploids respectively. However, as it is a question of increase in chromosome number of an already stabilized species, the original 32-chromosomal *M. sativa* has been described below as a diploid, the 48-chromosomal as a triploid, and the 64-chromosomal as a tetraploid. By the kind courtesy of Dr. LEVAN the chromosome counts as well as the fixation and staining of the microscopical specimens have been carried out in the Chromosome Laboratory in Svalöf. For this, and for his readiness in placing advice and suggestions at my disposal in the prosecution of the work, I hereby tender my cordial thanks.

MATERIAL AND METHODS.

A detailed description of the origin of the material is given in the above-mentioned paper of NILSSON and ANDERSSON (1941). The

original material was derived from three different stocks, two of which were pure *M. sativa*, while the third was the so-called Ultuna lucerne, which consists of a population of *M. sativa* × *falcata* crosses. Treatment of seedlings at the cotyledon stage with colchicine-agar produced some tetraploid plants ($2n = 64$), and these were propagated by means of cuttings. Crosses within these gave rise to three tetraploid seed plants. After crossing a tetraploid plant of pure *M. sativa* with a diploid plant of the Ultuna lucerne from one seed twins with a triploid complement of chromosomes ($2n = 48$) were obtained. At present there are thirty tetraploids and two triploids planted out in the trial field. Alongside these a number of clonal plants from diploid shoots taken from the original plants have been planted for comparison.

The results published by NILSSON and ANDERSSON (l. c.) from their investigations of the morphological characters include certain flower-measurements as well as the sizes of stomata and pollen-grains. Measurements have since been made of the length, breadth and thickness of the leaves, these being made on leaves from two stalks of each plant. On each stalk all the leaflets on the five lowest (oldest) sound leaves seated on the main stem have been measured. The leaf-length has been measured in whole millimetres and the breadth in tenths of a millimetre. The thickness has been gauged with a micrometer to one-hundreths of a millimetre, the measurements having been made on either side of the midrib over the broadest part of the leaf. Re-examinations of pollen-size and pollen-fertility have been carried out, for which purpose two specimens have been taken from each plant. The pollen-size has been measured with the help of an eye-piece micrometer at a magnification of × 800, one unit on the micrometer scale corresponding to 2,6 μ In evaluating the pollen-fertility at least 200 pollen-grains have been counted per specimen and the content of apparently normal grains has been computed. In 1942 the material was harvested and the plant weight as well as the relative weight of stem and leaf was determined in the green state. Specimens from both stem and leaf were dried in the drying plant of the Hay Department and subjected to chemical analysis for crude protein and crude fibre. For the cytological investigations flower-buds were fixed in Navashin's solution after pre-treatment in Carnoy's fluid, and the preparations were stained with crystal violet.

At the statistical reduction of the material use has been made, as a rule, of analysis of variance according to the methods described by BONNIER and TEDIN (1940). In comparisons between diploids and

tetraploids calculations have been made (1) on all diploid and tetraploid plants for which measurements had been effected, (2) on diploid and tetraploid clonal plants from the same original plant. These latter, of course, have the same genetic constitution and are therefore especially interesting to study. For this purpose two groups of clonal plants have been available. One group is derived from a pure *sativa* plant of Bulgarian lucerne. In the following account this group is called genotype *a*. The other group, genotype *b*, is derived from a plant of the

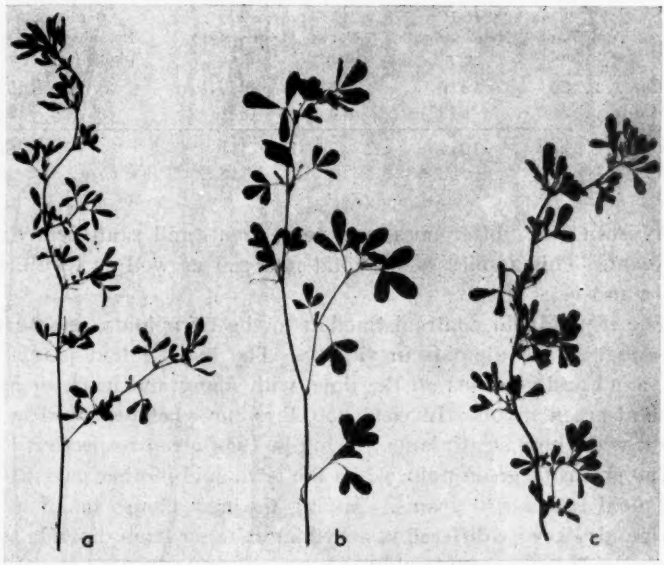

Fig. 1. Diploid father plant (*a*), triploid F_1 (*b*) and tetraploid mother plant (*c*) of *M. sativa*.

Ultuna lucerne, which is intermediate between *sativa* and *falcata*, although in mode of growth it approaches *sativa*.

RESULTS.

MORPHOLOGICAL INVESTIGATIONS.

During the first year of life the polyploid plants seemed to be more vigorous than the diploid, and on this account the question of whether increased productivity was to be expected as a result of the chromosome increase was answered in the affirmative by NILSSON and ANDERSSON.

During the succeeding years, however, the tetraploid plants have proved to possess distinctly inferior vitality to the diploid. Several of them died during the last winters and most of the survivals have shown very poor development with few and sparsifoliate stalks, and the plants have presented a scrubby appearance. New green shoots were very few during late summer or were entirely absent in most of the tetraploids, whereas they occurred abundantly in the diploids.

The plants were weighed in 1942 with the following results:

	Total material		Genotype *a*		Genotype *b*	
	No. of plants	Mean weight gm	No. of plants	Mean weight gm	No. of plants	Mean weight gm
Diploids	20	1616	3	2677	6	1452
Tetraploids ..	30	542	4	558	6	467
Difference		1074		2119		985
Variance		$53{,}88^{***}$		$18{,}57^{**}$		$11{,}16^{**}$

As seen, the differences are very great and statistically fully significant. This applies to the total material as well as to the genotypes *a* and *b*.

The triploids, in contradistinction to the tetraploids, appear to be fully equal to the diploids in vitality. The two triploid plants have been sound and vigorous all the time, with many and leafy stems and abundant green shoots. In yield, too, they have behaved well in competition with the parent plants, having in 1942 given respectively 1.000 and 750 grams of green pulp, while the tetraploid mother gave 210 and the diploid father 870 grams. Among the new clones taken in 1943 the triploids likewise differed in a striking manner from diploids as well as tetraploids by a considerably more rapid and vigorous growth.

The shape and size of the leaves vary very considerably in the different tetraploid plants. In some cases the tetraploids differ very much from the corresponding diploids by their considerably enlarged leaves, while in other cases they are indistinguishable in size from the diploids or are absolutely smaller than these. A difference that seems to be fairly regular, however, is the serration of the leaf-margin. In diploids this is usually limited to a couple of teeth at the leaf-apex itself, while in the triploids and tetraploids it usually occurs right down to the middle of the leaf.

Exact measurements of the leaves were undertaken in August, 1942, and around June 1st, 1943. Hence the first measurement was made on old, fully developed and to some extent lignified plants, while the second

Table 1. *Length, breadth and thickness of leaves in mm. in di-, tri- and tetra-ploid lucerne.*

	No. of measurements		Length		Breadth		Length : Breadth		Thickness	
	1942	1943	1942	1943	1942	1943	1942	1943	1942	1943
Total material										
Tetraploids	492	540	18,4	23,5	9,6	15,0	2,00	1,63	0,20	0,21
Diploids	366	360	20,1	23,6	7,3	11,0	2,85	2,19	0,15	0,16
Difference			— 1,7	— 0,1	2,3	4,0	— 0,85	— 0,56	0,05	0,05
Variance			$24{,}30^{***}$	< 1	$14{,}23^{***}$	$17{,}21^{***}$	$63{,}53^{***}$	$62{,}24^{***}$	$13{,}53^{***}$	$28{,}85^{***}$
Genotype a										
Tetraploids	114	120	19,8	25,1	11,3	17,2	1,83	1,48	0,22	0,23
Diploids	78	60	19,4	25,0	7,5	11,7	2,65	2,15	0,15	0,20
Difference			0,4	0,1	3,8	5,5	— 0,82	— 0,67	0,07	0,03
Variance			< 1	< 1	$11{,}54^{**}$	$28{,}55^{**}$	$30{,}99^{**}$	$71{,}31^{***}$	$7{,}96^{*}$	$46{,}11^{**}$
Genotype b										
Tetraploids	148	150	16,2	21,9	7,1	11,8	2,36	1,90	0,19	0,20
Diploids	146	150	21,5	22,2	7,9	10,5	2,76	2,16	0,14	0,14
Difference			— 5,3	— 0,3	— 0,8	1,3	— 0,40	— 0,26	0,05	0,06
Variance			$11{,}68^{**}$	< 1	< 1	$4{,}25$	$7{,}93^{*}$	$5{,}85^{*}$	$10{,}34^{*}$	$18{,}54^{**}$
Triploids	60	60	22,6	33,1	10,3	19,7	2,21	1,69	0,18	0,21
Tetraploid mother	30	30	15,5	26,4	8,4	16,4	1,79	1,65	0,16	0,22
Diploid father	30	30	18,0	22,2	6,0	11,3	3,08	1,99	0,15	0,16

was carried out when the plants were young and sappy. The absolute dimensions were a little different on the two occasions, but the different plants show good agreement amongst themselves. The correlation between the measuring-results for the two years for the length : breadth ratio of the leaf is $0{,}78^{***}$.

The results of the leaf measurements are given in Table 1.

It is evident from this that the length of the leaf has not undergone any definite alteration as a result of the chromosome doubling, though it shows a certain tendency to diminution, especially in genotype *b*. The breadth, on the other hand, has substantially increased on the average for the whole material. This also appears very clearly in

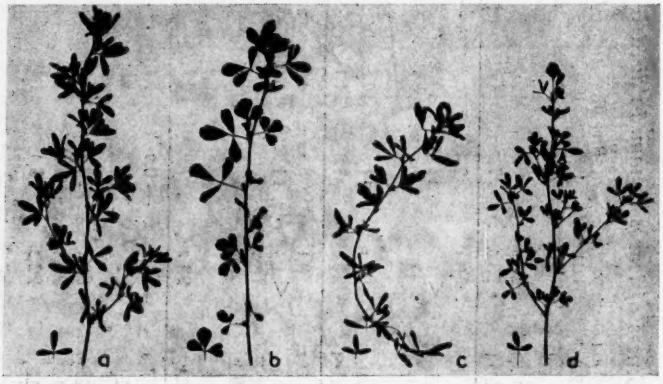

Fig. 2. Diploid (*a*) and tetraploid (*b*) of genotype *a* as well as diploid (*c*) and tetraploid (*d*) of genotype *b*.

genotype *a*, whereas no change is discernible in genotype *b*. Thus, leaf shape has altered more in genotype *a*. The length : breadth ratio of the leaf has fallen here considerably in the tetraploids as compared with the diploids, while the change in genotype *b* is less and of a more indefinite character. This means that, while leaf shape and size in the diploids are in very close agreement in the two genotypes, the tetraploids differ much from one another in these respects. The thickness of the leaves has increased throughout by 30—50 per cent following transition from diploid to tetraploid stage.

The leaves of the triploids are both longer and broader than those of the two parents, and the length : breadth relation lies between the corresponding ratios of the parents. In leaf-thickness the triploids agree most closely with the tetraploids (Fig. 1).

The weight ratio between stem and leaf varies to a considerable extent from plant to plant. Plants were weighed in the green state and gave the following values:

	Total material		Genotype *a*		Genotype *b*	
	No. of plants	Leaf : Stem	No. of plants	Leaf : Stem	No. of plants	Leaf : Stem
Tetraploids	19	0,78	3	0,99	5	0,60
Diploids	13	0,65	3	0,46	5	0,75
Difference		0,13		0,53		— 0,15
Variance		3,28		7,60*		1,81
Triploids	2	0,68				
Tetraploid mother..	1	0,69				
Diploid father	1	0,82				

On an average, thus, the tetraploids show a somewhat greater leaf-weight relative to the stem than the diploids. On account of the great

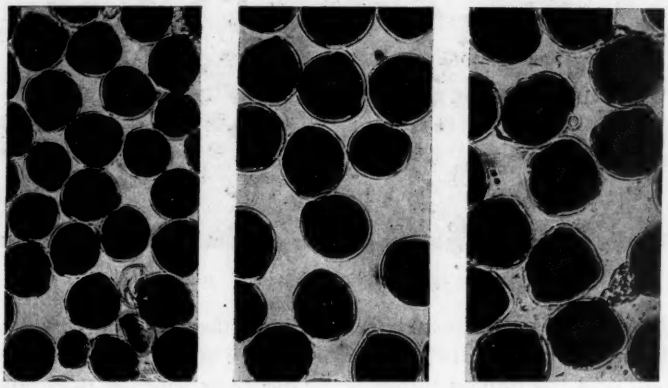

Fig. 3. Pollen-specimens of di-, tri- and tetra-ploid *M. sativa*. (× 300.)

variance, however, this difference is very uncertain. Still, genotype *a* displays a very distinct and relatively definite tendency in this direction, while genotype *b* agrees very closely with the corresponding diploids. The great difference between the tetraploids of genotypes *a* and *b* accords, of course, with expectation in view of the great differences in leaf-size. The triploids differ in this respect relatively little from the parent plants, but agree with the tetraploid mother.

A very striking difference between diploids, triploids and tetraploids makes its appearance in respect of pollen-size. This increases throughout with high chromosome number. Certainly there is some

variation between the different mean values of the plants, but for diploids and tetraploids these fall within quite separate ranges of variation. Thus, the means for the diploids varied between 12,45 and 14,45 units (1 unit = 2,6 μ) and for the tetraploids between 15,95 and 18,80 units. The following means have been obtained:

	Total material		Genotype *a*		Genotype *b*	
	No. of measurements	Mean units	No. of measurements	Mean units	No. of measurements	Mean units
Tetraploids	180	17,17	40	17,09	50	17,40
Diploids	120	13,81	20	14,90	50	13,50
Difference		3,36		2,19		3,90
Variance		155,78***		17,92**		90,57***
Triploids	20	16,42				
Tetraploid mother..	10	17,35				
Diploid father	10	12,45				

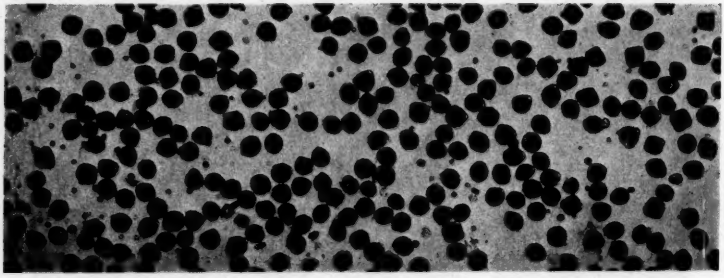

Fig. 4. Pollen specimens of triploid *M. sativa*. (× 80.)

Larger pollen is, thus, characteristic of the polyploids irrespective of whether they belong to genotype *a* or *b*. The difference between the triploids and the diploid father is greater than between them and the tetraploid mother.

FERTILITY.

As regards pollen-fertility the variation between different plants is very great. However, on the average, the polyploids have a very high content of normal pollen, while the pollen-fertility of the diploids is remarkably low in some cases. The normal pollen-content varied in the diploids between 46 and 95,5 per cent and the mean is 75,2 per cent. For the tetraploids the corresponding extreme values are 73 and 97 with 86,6 per cent as mean. Statistically, the difference between the means, 11,4* per cent, is relatively significant. In plants of genotype *a*

the pollen-fertility averages 51,3 and 82,8 per cent for diploids and tetraploids respectively and the difference is fully significant (variance quotient: 177,78***). For genotype *b* the corresponding figures for diploids and tetraploids are 89,4 and 81,6 per cent, the tetraploids showing a somewhat inferior fertility to the diploids, but the difference is very uncertain. The triploids, too, show a very high pollen-fertility, viz. 94 and 95 per cent good pollen, while the corresponding value for the diploid father is 79 and for the tetraploid mother 84,5 per cent.

It has not been possible to obtain any exact figures for the seed-setting, as during both 1942 and 1943 this was exceedingly bad in diploids as well as polyploids on account of the very unfavourable weather for seed-setting. Still, it seems as if the seed-setting power in the tetraploids was considerably inferior to that of the diploids. The triploids also seem to set less seed than the diploids, though they show a distinct superiority in this respect as compared with the tetraploids.

CHEMICAL INVESTIGATIONS.

Dried specimens of leaves and stems have been analysed for their content of crude protein and of crude fibre, the following means having been obtained:

	No. of plants	In percentages of dry matter: Crude protein leaf	Crude protein stem	Crude fibre leaf	Crude fibre stem
Total material:					
Tetraploids	18	27,81	16,94	11,12	46,89
Diploids	13	25,98	16,21	9,41	48,35
Genotype *a*					
Tetraploids	4	29,80	14,33	11,38	48,08
Diploids	3	26,80	14,97	9,40	48,70
Genotype *b*					
Tetraploids	5	25,24	17,46	9,96	47,88
Diploids	5	27,22	18,36	9,32	49,40
Triploids	2	23,9	21,7	8,6	50,2
Tetraploid mother ..	1	27,0	14,3	10,3	46,8
Diploid father	1	24,1	19,5	8,7	45,1

In the leaves some tendency to higher content of crude protein as well as of crude fibre is noticed. This tendency is especially distinct in genotype *a*. The variation between different plants is, however, rather considerable and therefore the differences are in no case significant. The differences are still less in the case of the composition of the stem. Nor do the triploids differ to a noteworthy extent from the

parent plants in this respect. These results from a few analyses must be regarded as very preliminary and uncertain, but they would seem to justify the assumption that no considerable changes in the chemical composition have arisen through chromosome increases, which is of importance from a practical breeding point of view.

CYTOLOGICAL INVESTIGATIONS.

Besides chromosome counts on root-tip material a study has also been made of meiosis in a number of plants. Although the meiotic fixations in general were not sufficiently advantageous to allow of a detailed analysis, the general course of meiosis could be followed on broad lines. Within all the examined plants univalents occur, though in different frequencies. The univalents were studied in side view of first metaphase, when they lay outside the equatorial plate. The frequencies given are naturally minimum figures, since some univalents are probably concealed within the plates. The univalents could also be studied at first anaphase, now in the form of laggards between the anaphase groups. Whole metaphase plates could rarely be analysed. In a number of cases, though, trivalents could be observed with certainty. Chromosome complexes that are apparently quadrivalents have also been observed.

Remarkably often the diploids showed disturbances in the course of meiosis. Instead of solely bivalents there often occurred a number of univalents and in a few cases also multivalents, trivalents being then more often observed than quadrivalents. The univalent frequency was fairly constant in every plant examined, but varied considerably between different plants. As an example genotypes *a* and *b* (Table 2) may be cited. The former had relatively few univalents (one univalent in every fifth cell), the latter had a very high univalent frequency (up to six univalents per cell, only every tenth cell was free from univalents). All the meiotic fixations were made on the same occasion and therefore the differences in univalent frequency can scarcely depend upon differences in the external conditions. In the diploids the bivalents usually had rod form. Only in very rare cases were rings observed.

The commonest configuration during meiosis in the tetraploids was bivalents, but both univalents and quadrivalents occurred. Table 2 shows that the univalent frequency also varied considerably among the tetraploids. In genotype *a* the tetraploid had a higher frequency of cells with univalents than the original diploid, while the relation was the reverse in genotype *b*. As in the diploids, the bivalents were usually

rod-shaped. In one analysed plate (Fig. 5 *d*) one ring bivalent was observed, while the majority were of the rod shape. Quadrivalents were more common than in the diploids. Thus, the analysed cells contained nine quadrivalents, all of which were ring-shaped. The low frequency of ring-shaped bivalents among the diploids suggests that some of the chromosome complexes having the appearance of quadrivalents may actually be two bivalents that have united secondarily. In view of the shape of the bivalents among the diploids it might be expected that chains would have been the most common quadrivalent

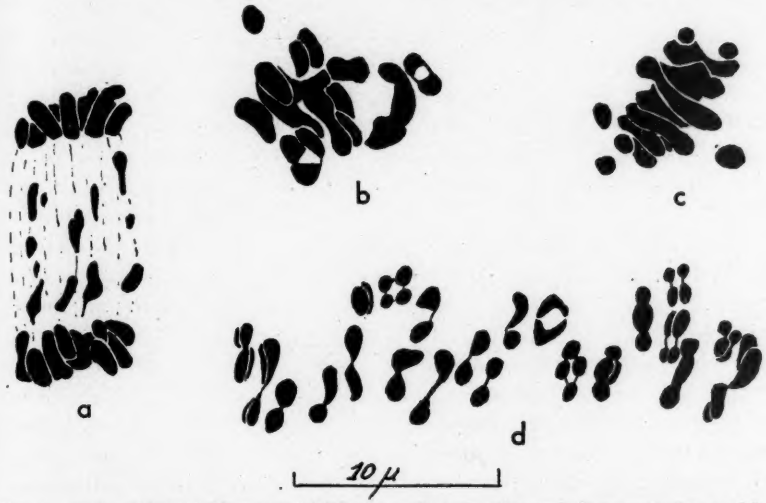

Fig. 5. *a, b, c* diploid *M. sativa* × *falcata*, *a* first anaphase, *b* first metaphase with 1 univalent and 1 trivalent, *c* first metaphase with 6 univalents, *d* first metaphase of tetraploid *M. sativa*, apparently $9_{IV} + 14_{II}$.

type among the tetraploids. Chain quadrivalents were, however, not observed in any case.

The triploids had a remarkably regular meiosis. Judging from the low univalent frequency (1—2 univalents in 29 % of the cells) and the absence of multivalents, up to 24 bivalents could be formed within the triploids. It has also been possible to count 24 elements in the polar views of certain plates. This implies a high degree of autosyndesis. The meiosis in the triploids affords good support for the view that *Medicago sativa* is already tetraploid in its spontaneous form.

It will be seen from Table 2 that the disturbances of first anaphase within the different types are closely connected with the univalent

TABLE 2. *Frequency of different numbers of univalents at first metaphase and of normal and disturbed first anaphase.*

No. of univalents at 1st metaphase	Genotype *a*		Genotype *b*		Triploids	Crosses between two tetraploids. *M. sativa* 2n = 64
	dipl.	tetrapl.	dipl.	tetrapl.		
0	80 %	53 %	11 %	38 %	71 %	49 %
1	20 »	35 »	44 »	23 »	23 »	34 »
2	—	12 »	22 »	28 »	6 »	13 »
3	—	—	14 »	9 »	—	3 »
4	—	—	3 »	2 »	—	1 »
5	—	—	3 »	—	—	—
6	—	—	3 »	—	—	—
1—6	20 %	47 %	89 %	62 %	29 %	51 %
No. of cells examined	46	129	36	64	34	192
1st anaphase:						
Normal	80 »	59 »	11 »	32 »	75 »	50 »
Disturbed	20 »	41 »	89 »	68 »	25 »	50 »
No. of cells examined	10	58	37	28	57	66

frequency at first metaphase. Besides lagging univalents, real bridges also occur in some cases between the anaphase groups.

The cytological study of the material will be continued.

DISCUSSION.

As was found to be the case with the majority of products of doubling among spontaneous species, e. g. flax (LEVAN, 1942), the vitality optimum of *Medicago sativa*, judging from the present material, is exceeded at a doubling of the chromosome number. The plants become smaller and poorer in leaves, and the vitality seems to become impaired in consequence of the chromosome increase. The 48-chromosomal plants, though, appear to be closer to the optimum. The vitality optimum associated with a triploid number of chromosomes has also been shown for other species, e. g. sugar beets (PETO and BOYES, 1940). However, the luxuriant growth and good vitality of the triploids need not be exclusively due to the triploidy, since these plants consist of seed progeny from a cross, which may conceivably have contributed to their exuberance. The result is therefore rather to be regarded as a joint effect of polyploidy and heterosis. The question is then whether a heterosis that has arisen through crossing a tetraploid with a diploid is more constant and persistent in the following generation than a heterosis

that comes from intercrossing diploids. An answer to this question can only be obtained by further investigations. In practical plant breeding, however, there are possibilities of obtaining positive results if triploid plants are produced by crossing diploids and tetraploids. To be of service in practice a lucerne stock must, however, show satisfactory seed-setting. How the plants behave in this respect has not emerged during the years the investigations have been in progress, partly on account of unfavourable external circumstances, partly owing to the fact that the two available triploid plants are twins and no true cross fertilization could therefore be effected. There are, however, possibilities of obtaining triploid lines with constant chromosome number and full fertility, as everything goes to show that these triploids are in reality hexaploids. Arguing in favour of this is the common occurrence of *Medicago* species with $2n = 16$. The appearance of univalents, trivalents and quadrivalents as well as of disturbances at the anaphase of meiosis in the diploids also indicate that a tetraploid species is concerned here. Meiosis in the 48-chromosomal lucerne is at least as regular as in the 32-chromosomal one, and the triploids have very fine pollen with well-filled grains of equal size (Fig. 4). Since about 100 seeds per plant were obtained in 1943, there exists in any case some degree of fertility.

The *gigas* character of the polyploids is very unequally expressed in the different genotypes. Measurements performed by NILSSON and ANDERSSON (1941) show that the length and breadth of both sepals and petals have augmented as a result of the chromosome increase in genotype *a*, and that in the majority of cases the increase was statistically demonstrable. In genotype *b* all flower-measurements with the exception of pedicel length give lower values for the tetraploids than for the diploids, although the differences, except for the flower length, are not statistically significant. This is in good agreement with the measurements of size and shape of leaf given in the present paper, the leaves in genotype *a* having been enlarged rather considerably in consequence of the increase in chromosome number, while genotype *b* has not undergone any noteworthy alteration in respect of the majority of characters. The only features in which a *gigas* character appears throughout in the two genotypes are leaf-thickness and pollen-size. Whether the differences between genotype *a* and *b* are due to the *falcata* genes entering into genotype *b*, or whether these differences can also arise within different lines of pure *M. sativa*, cannot be decided with the aid of the present material.

The changes that occurred in genotype *a* following the chromosome doubling are in very good accordance with the results PIRSCHLE (1942 a) has come to in his investigations on some different species of plants. He has consistently found an increase in leaf-surface and leaf-thickness and a reduction of the length : breadth ratio of the leaves on transition from the diploid to the tetraploid stage. In spite of the regular *gigas* characters he is able to establish the fact that the autopolyploid forms need not be either longer or heavier than the corresponding diploids, a fact that is clearly confirmed by the present investigations on *Medicago*. He also contends that the different degrees of expression shown by *gigas* characters in different cases indicate that it is not immaterial what genes or gene combinations are doubled. The comparison between the results of the chromosome doubling in genotype *a* and genotype *b* of *Medicago* also shows very clearly that different sets of genes react essentially differently to the doubling.

Not only changes in the quantitative yield but also qualitative changes, thus changes in the chemical composition and especially in nitrogen content, are of interest to the practical plant breeder. Investigations hitherto carried out to ascertain the effect of the polyploidy on the chemical constitution have given somewhat contradictory results. As a rule, however, the changes have been very small and have generally fallen within the limits of error (PIRSCHLE, 1942 b). LEVAN (1943), in investigations on sugar beets and mangels, has found that the polyploid forms of these kinds (varieties) of plants do not constitute any direct advances in respect of quality, but that, on the other hand, neither have they brought about any qualitative impairment. The analyses performed here on *Medicago sativa* to determine the crude protein and crude fibre contents also show that very small changes attend a transition from diploid to tetraploid stage. The prospects of producing forage plants of a qualitatively higher kind by chromosome doubling therefore seem to be very small. On the other hand, the risk of any considerable impairment of the quality characters is doubtless very small.

In an investigation relating to the cytological conditions in, among others, *Medicago* FRYER (1930) found in *Medicago media* PERS. certain irregularities in meiosis in the form of a straying of chromosomes at the second metaphase and a lagging of chromosomes at the second anaphase. These phenomena are considered by him to depend on the fact that *M. media* is to be regarded as a hybrid. The meiotic differences in the genotypes *a* and *b* in the present experiments would accordingly be explained on the basis that genotype *a* is a pure *M. sativa*, while

genotype *b* is a hybrid between *M. sativa* and *M. falcata*. Whether this is actually the case cannot, however, be conclusively determined with the present material.

A remarkable feature is that within the material examined no correlation could be detected between irregularity in meiosis and pollen-fertility. In some cases, e. g. in the diploids of genotype *b*, where meiotic disturbances occur in very great frequency, the pollen-fertility is very high. Conversely, in for instance the diploids of genotype *a* the pollen-fertility is low in spite of the fact that in general the meiosis seems to run a perfectly normal course. It therefore seems as if minor irregularities in meiosis do not have an appreciable effect on the development of the pollen. Other factors, lethal genes or suchlike, must also be presumed to occur and to have a depressive effect on the pollen-fertility.

SUMMARY.

Investigations have been carried out on diploid *Medicago sativa* and *Medicago sativa* × *falcata* as well as on triploid and tetraploid forms of these obtained by colchicine treatment.

The tetraploid plants have regularly shown an inferior vitality to the diploids. On the other hand, the triploid plants present a very vigorous appearance, probably owing to the joint effects of polyploidy and heterosis.

In respect of leaf-shape the chromosome doubling has brought about highly different effects within different lines. For instance, within a line of pure *M. sativa*, genotype *a*, the leaf-surface has been greatly enlarged, the breadth having increased. Within a line from *M. sativa* × *falcata*, genotype *b*, no change in size of leaf is detectable. The triploids show greatly enlarged leaves. The leaf-thickness has constantly increased in consequence of the polyploidy. The pollen-grains are larger throughout in the tetraploids than in the diploids. In this respect the triploids occupy an intermediate position that approaches the tetraploids.

The pollen-fertility is very good in both triploids and tetraploids.

Chemical analysis has disclosed no notable difference in contents of crude protein and crude fibre between diploids and polyploids.

At meiosis in the diploids, besides bivalents, there occur univalents, trivalents as well as quadrivalents. Disturbances of anaphase often occur. The occurrence of univalents and the disturbances of anaphase seem to be in close relation to each other. These phenomena corroborate the

assumption that in the spontaneous *Medicago sativa* we have a tetraploid species. The meiosis in triploids and tetraploids seems to be as regular as in the diploids. No correlation has been found between meiotic disturbance and pollen-fertility.

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THE INFLUENCE OF SEED SIZE AND HULLS ON X-RAY SUSCEPTIBILITY IN CEREALS

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IN the extensive experiments carried out at the Swedish Seed Association in connection with the X-ray induction of viable mutations, a series of methodological problems are also being successively investigated. The questions to be answered in this paper concern especially two properties of the seed material: the size of the seeds to be treated and the possession of hulls (naked *versus* covered varieties). The influence of seed size has chiefly been examined in wheat, the influence of attached hulls in barley and oats.

The irradiation work was performed at the Radiophysical Institute of Karolinska Sjukhuset, Stockholm (Director: Professor R. SIEVERT) under the supervision of Dr. A. FORSSBERG, to whom we are indebted for valuable help and discussions. The seeds were X-rayed on February 26—27th, 1943.

SEED SIZE AND X-RAY SUSCEPTIBILITY.

Wheat. — Well-ripened and normal seed material of Svalöf's Kolben Spring Wheat and Svalöf's Winter Wheat Velvet 0700 (harvested in 1942) was divided into four size-classes, the first-mentioned variety by the use of sieves with a mesh-width of 1,75, 2,00, 2,25 and 2,50 mm., the latter variety by sieves having a mesh of 2,00, 2,25, 2,50 and 2,75 mm. Consequently, the seeds do not generally reach the same size in Svalöf's Kolben Wheat as in 0700. The thousand-kernel weight of unsifted Kolben Wheat was 33,3 gr., that of Velvet Wheat 37,5 gr. 100 seeds of each size group were given 10.000 and 20.000 r-units (176 kV, 4 ma., 1840 r/min.). The average water content at the time of irradiation was 11,7 % for Svalöf's Kolben Wheat and 12,3 % for 0700, the large seeds generally having a somewhat higher water content than the small ones.

On March 24th all X-rayed samples, as well as parallel controls, were sown under uniform conditions in boxes with similarly moistured soil. Air temperature + 20° C. For further details respecting method the reader is referred to the papers by FRÖIER, 1941, and FRÖIER and

TABLE 1. *Germination and seedling growth in wheat varieties after irradiation.*

	Sieve 1,75 mm.	Sieve 2,00 mm.	Sieve 2,25 mm.	Sieve 2,50 mm.	Sieve 2,75 mm.
Germination tests					
Svalöf's Kolben Wheat					
Control	97 % (1)	97 % (1)	94 % (1)	95 % (1)	—
10.000 r.	86 » (0,89)	95 » (0,98)	97 » (1,03)	100 » (1,05)	—
20.000 r.	5 » (0,05)	10 » (0,10)	14 » (0,14)	37 » (0,39)	—
Svalöf's Velvet Wheat 0700					
Control	—	96 % (1)	97 % (1)	97 % (1)	97 % (1)
10.000 r.	—	95 » (0,99)	96 » (0,99)	98 » (1,01)	95 » (0,98)
20.000 r.	—	? ?	10 » (0,10)	10 » (0,10)	18 » (0,19)
Seedling growth					
Svalöf's Kolben Wheat					
Control	171,1 mm. (1)	189,4 mm. (1)	198,1 mm. (1)	200,4 mm. (1)	—
10.000 r.	86,0 » (0,50)	99,7 » (0,53)	110,5 » (0,56)	112,7 » (0,56)	—
20.000 r.	26,8 » (0,16)	32,9 » (0,17)	41,6 » (0,21)	30,3 » (0,15)	—
Svalöf's Velvet Wheat 0700					
Control	—	192,4 mm. (1)	192,8 mm. (1)	194,1 mm. (1)	202,5 mm. (1)
10.000 r.	—	86,2 » (0,45)	96,3 » (0,50)	105,2 » (0,54)	100,0 » (0,49)
20.000 r.	—	? (?)	30,4 » (0,16)	45,0 » (0,23)	29,7 » (0,15)

GUSTAFSSON, 1941. Only those seedlings whose coleoptiles had penetrated the soil surface were counted as normal. The growth of their first leaf was measured on April 3rd—5th.

In a recent paper FREISLEBEN and LEIN (1943) have for various reasons objected to this method of determining the X-ray effect. We regard it, however, as sufficiently reliable, and as the only one practical in comprehensive experiments. Our laboratory experiments are not designed as a substitute for field work, but merely to indicate the irradiation limits to be used in the subsequent field tests. Indeed, we doubt whether laboratory methods could be worked out which are capable of dispensing entirely with field trials.

As seen from Table 1, germinability increases with greater seed size, especially in Kolben Spring Wheat (after 10.000 r from 86 to 100 %, and after 20.000 r from 5 to 37 %), but an increase is also noticeable in Velvet Wheat 0700 at 20.000 r. Unfortunately, the smallest-sized seed sample had to be discarded at this dosage owing to some mistake at the time of irradiation.

As to the second property (leaf growth), this undergoes a steady increase already in the untreated controls, from 171 to 200 mm. in Svalöf's Kolben Wheat and from 192 to 203 mm. in Velvet 0700. After an irradiation of 10.000 r, however, the leaf growth increases more rapidly with greater seed size than in the control, the relative values being 0,50, 0,53, 0,56 and 0,56 for Kolben Wheat (the control put down as 1). After 20.000 r-units we find a similar increase up to the largest seed size but one, the relative values being 0,16, 0,17, 0,21, *0,15*. In Velvet Wheat 0700 the relative values are 0,45, 0,50, 0,54, *0,49* after 10.000 r-units, and ?, 0,16, 0,23, *0,15* after 20.000 r-units. Consequently, there is a rather conspicuous increase in growth up to a certain point, after which a retardation sets in. The cause of this latter phenomenon is evidently that at least after the highest dosage (20.000 r) a number of greatly damaged seedlings are just capable of penetrating the soil surface if the embryos are very large, but this is impossible if the seeds and the embryos are smaller in size.

For a correct interpretation of these results it is necessary to know the exact changes of the embryo size in different seed material. If the larger seed size only depends upon an increase in endosperm size, the altered X-ray susceptibility would be a secondary property of nutrition conditions rather than a primary effect of the embryo itself. In wheat this question may immediately be answered by measurements under the microscope of the embryo size, i. e. the distance from the tip of the

coleoptile to the apex of the coleorhiza. The result of the measurements is shown in the following survey:

	Kolben Spring Wheat	Velvet Winter Wheat 0700
Sieve 1,75	$M_{50} = 1{,}610 \pm 0{,}0221$ mm.	—
» 2,00	$M_{50} = 1{,}697 \pm 0{,}0224$ »	$M_{50} = 1{,}816 \pm 0{,}0365$ mm.
» 2,25	$M_{50} = 1{,}754 \pm 0{,}0192$ »	$M_{50} = 1{,}879 \pm 0{,}0275$ »
» 2,50	$M_{50} = 1{,}839 \pm 0{,}0217$ »	$M_{50} = 2{,}047 \pm 0{,}0291$ »
» 2,75	—	$M_{50} = 2{,}059 \pm 0{,}0311$ »

These figures illustrate the parallel increase of embryo and seed size. Consequently, we may conclude that the change in X-ray susceptibility within a strain is largely due to the embryo size itself, in such manner that the smaller an embryo is, the more susceptible it is to X-rays, and *vice versa.*

HULL OCCURRENCE AND X-RAY SUSCEPTIBILITY.

Barley. — In this cereal naked and covered varieties are known. Carl Engström Ltd., Eslöv, has bred a six-row variety lacking hulls and suited for Swedish conditions. This variety has been compared as to X-ray susceptibility with Brio (a hull-covered six-row variety) and Maja (a covered two-row variety). In addition, seeds of an F_6 progeny of »Engström's Hulless × Brio» were irradiated. In this cross no other selection has been undertaken in F_2—F_6 but for naked seeds. Consequently, seeds of this progeny lack hulls but in other respects they represent a mixture of genes and chromosomes from Engström's Hulless and Brio.

Seeds of these varieties were given doses from 2.500 up to 20.000 r, with 100 seeds in each sample. They were sown on March 13th, and on March 23rd the length of the first leaf was measured. The water content at the time of irradiation varied in the four sets of material only from 11,8 % to 12,2 %.

The results are given in Table 2. — First the germination: This is highly reduced in the naked material. The cross »Engström's Hulless × Brio» behaves about the same as the hulless mother strain. If anything, it is slightly more susceptible.

In this series of experiments no certain difference is met with between the two-row and the normal six-row variety (Brio), this in contrast to earlier experiments, where the six-row variety Edda was examined.

TABLE 2. *Germination and seedling growth in covered and hulless varieties of barley.*

	Maja (Two-row barley)	Brio (Six-row barley)	Engström's Hulless (Six-row barley)	Engström's Hulless×Brio (Six-row barley)
Germination				
Control	100 % (1)	99 % (1)	96 % (1)	86 % (1)
2.500 r	96 % (0,96)	100 % (1,01)	94 % (0,98)	89 % (1,03)
5.000 r	98 % (0,98)	97 % (0,98)	96 % (1,00)	83 % (0,97)
10.000 r	84 % (0,84)	97 % (0,98)	45 % (0,47)	36 % (0,42)
15.000 r	41 % (0,41)	30 % (0,30)	—	2 % (0,02)
20.000 r	12 % (0,12)	8 % (0,08)	—	—
Seedling growth				
Control	173,7 (1)	178,5 (1)	171,1 (1)	156,5 (1)
2.500 r	170,3 (0,98)	167,5 (0,94)	164,6 (0,96)	137,2 (0,88)
5.000 r	141,6 (0,82)	153,9 (0,86)	138,0 (0,81)	129,6 (0,83)
10.000 r	89,8 (0,52)	84,5 (0,47)	60,3 (0,35)	48,4 (0,31)
15.000 r	52,8 (0,30)	56,3 (0,32)	—	(52,0)
20.000 r	33,8 (0,20)	(78,3)	—	—

As to leaf growth the naked varieties suffer considerably more from irradiation than the covered ones. The relative length values (the controls set as 1) after 10.000 r are Maja: 0,52, Brio 0,47, and for the naked varieties Engström's Hulless and »Engström's Hulless × Brio»: 0,35 and 0,31 respectively.

These data show, beyond reasonable doubt, that the possession of hulls is no negligible factor in the irradiation work. In spite of the extremely hard rays used in these experiments, the hulls evidently protect the embryos.

As in previous investigations (cf. GUSTAFSSON, 1944), the »critical dosage» for Maja barley should lie at about (15.000—)20.000 r, that for the naked varieties is lower and should lie at about 12.500 r.

Oats. — Practically all commercial varieties of oats possess hulls tightly enclosing the kernels. It is an easy matter, however, to remove these with a pair of forceps, in the same way as is done in seed control work when determining the hull percentage (or kernel percentage) of a seed sample. In order to obtain as uniform conditions as possible only seeds of a strictly similar size (sieve 2,25 mm.) were irradiated. The water content at the time of irradiation was 10,6 % for the normal and

10,8 % for the hulless material. The variety used was Segerhavre (Victory Oats). The seeds were given 10.000 and 20.000 r, and the material (100 seeds in each series) was sown on March 19th. The length of the first leaf was measured on April 1st.

TABLE 3. *Germination and seedling growth in normal and hulless material of Victory Oats.*

	Germination		Seedling growth	
	Normal material	Hulless material	Normal material	Hulless material
Control	97 % (1)	83 % (1)	155,0 (1)	154,1 (1)
10.000 r	95 % (0,98)	81 % (0,98)	130,2 (0,84)	120,4 (0,78)
20.000 r	38 % (0,39)	10 % (0,12)	61,4 (0,40)	53,9 (0,35)

The germination of the seeds with removed paleae was markedly inferior to that of the normal material (Table 3). Evidently the procedure used occasionally damages the embryos. The relative values show, however, that the X-ray susceptibility increases more rapidly in naked than in normal material.

The leaf length was identical in both controls, but after 10.000 and 20.000 r-units it was slightly smaller in the naked than in the normal seed series.

Consequently, there is an evident protection of the embryos by the hulls in oats as well as in barley. The X-rays are more effective in naked than in covered material.

SUMMARY.

In this paper two seed properties have been examined with regard to their possible significance in X-ray induction of mutations. It was found (1) that an increase in seed size, and accordingly in embryo size, causes better germination and more vigorous growth after the X-ray dosages applied, except after the highest dose, when the average leaf length decreases, and (2) that the hull covering of barley and oats makes the seeds less susceptible to irradiation. The latter result was obtained after a comparison of covered and naked varieties in barley, as well as of normal and hulless seeds in Victory Oats.

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IS MY TERMINOLOGY OF THE APOMICTIC PHENOMENA OF 1940 INCORRECT AND INAPPROPRIATE?

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THE main features of my proposal (FAGERLIND, 1940 a) of a revised classification and terminology of those processes which are associated with apomixis in higher plants can be summarized as follows.

Apomixis in higher plants is connected (agamospermy) or unconnected with producing of seeds. Agamospermy followed by an alternation of generations is denoted by agamogony. If no alternation of generations occurs, sporophyte initials are formed from nucellar or other sporophytic cells (nucellar embryony). Agamogony is based upon two processes, *viz.* formation of gametophytes without reduction of the chromosome number (apomeiosis) and formation of sporophytes without fertilization. The first process occurs in three different ways, the results of which are as follows: (1) diplospory, *i. e.* the unreduced number of chromosomes originates from semi-heterotypic division followed by formation of restitution nuclei; (2) semi-apospory, *i. e.* the unreduced number of chromosomes is caused by pseudohomeotypic division; and (3) apospory, *i. e.* meiosis and its »variations» are completely lacking. In the latter case, a gametophyte initial may lack (somatic apospory) or it may show the character of archesporial cells (generative apospory). It should be emphasized that somatic and generative apospory are connected by transition forms and, furthermore, that diplospory, semi-apospory, and generative apospory are the result of a dissimilarly pronounced »degree of meiotization». In some way, they thus represent three fractions of a variation scale (cf. further FAGERLIND, 1940 a and b. 1944).

GUSTAFSSON (1944) states that this system »consisted in part of misused terms and for that reason cannot be accepted; in part — when it was not incorrect — it was unsuitable from a general point of view», and he subjects it to criticism biting in words yet insignificant in content. He also attacks STEBBINS (1941), who abandoned his earlier termin-

ology in order to accept my system without reservation. Since anyone not fully conversant with the subject might find GUSTAFSSON's criticism justified, a reply seems to be indispensable. Below, the various points of the criticism will be treated in their proper turn.

(1) GUSTAFSSON states — just as WINKLER (1942) did earlier — that »my» term apomixis even includes the »amixis phenomenon». Since my terminology, my definitions, and my classification concern the higher plants (cf. my introduction and my table-heading, 1940 a), which completely lack amixis, the criticism is irrelevant. WINKLER, GUSTAFSSON, and myself agree completely as to the meaning of apomixis. [WINKLER's criticism has already been answered in a paper on *Elatostema* (FAGERLIND, 1944), accepted for publication by the Royal Swedish Academy of Science.]

(2) GUSTAFSSON emphasizes that my newly introduced term agamogony has previously been applied by HARTMANN (1929) in quite a different meaning. I admit that I had forgotten or simply never observed this fact. Here — in this point alone — criticism is justifiable. As a term is required, I now venture to propose apogamogony. Organisms with apogamogony are conveniently called apogamogones.

(3) GUSTAFSSON becomes most verbose when criticizing the manner in which I apply the term diplospory and the consequences of its use. In 1940, I mainly pointed out that I assume a restriction. This is however, as will be shown in the following, rather of apparent than of real character. At that time, I also showed that it is objectionable to change without reason the meaning of terms introduced earlier. On the other hand, it must be considered a meritorious action to »purify» old definitions when new progress in science demands it. (The text of the original definition appears to be completely in variance with the author's real intention, with the exemplifications delivered by him, with the limitation of previous terms, etc.) Is it accidental that GUSTAFSSON, who cites literally parts of my statement, just leaves out the words, replacing them by dots, which explain when the changes must be regarded as permissible?

GUSTAFSSON does not mention the point that I employ the term generative apospory in another meaning (in fact apparently, only) than does CHIARUGI. If he had indicated the »mistake» just here, he would have been obliged to cancel completely the term diplospory which he himself has applied in recent years. If we adopted GUSTAFSSON's methods of interpretation, diplospory and the older term generative apospory should be regarded as synonyms.

The application of the mentioned terms in the way proposed by the author should be considered not only justifiable but, moreover, desirable. In order to understand this, it may be recalled that the old term apospory (VINES, 1878; BOWER, 1884/86, 1887) refers to the formation of gametophytes from other sporophytic cells than spores. GUSTAFSSON and some of his predecessors reserve this term for those cases in which the gametophytes arise from cells which are not archesporial cells or their derivatives. *Thus, the meaning of the old term has been restricted, or it has not been clearly understood which cells of the higher plants should be regarded as spores.*

CHIARUGI (1926) divided apospory into two classes, *viz.* generative and somatic apospory (properly expressed, aposporia goneale and somatica), dependent on whether the gametophyte initials or their mother-cell possess or are devoid of the character of archesporial cells. He assumes that the diploid »dyad-cells», being gametophyte initials in certain apogamogones, are not spores but pseudospores. It becomes clear that in essence CHIARUGI's meaning is: *generative apospory = formation of gametophytes from archesporial cells or their derivatives which lack the character of spores.*

Likewise, EDMAN defines the term apospory in the initial way. He assumes, however, that not all the cases which, according to CHIARUGI's exemplification, range to generative apospory have to do with apospory. On the contrary, here we are concerned with diplospory. Although the chromosome number of the gametophyte initial is not reduced, it is considered to have the nature of spores. Thus, EDMAN says, it is not only analogous but homologous to a spore. Correspondingly, EDMAN's meaning is: *diplospory = formation of gametophytes from non-reduced spores.*

In his critical paper, GUSTAFSSON (1944) — E scheme — defines diplospory in agreement with this meaning and, moreover, in full agreement with the present writer's sharply criticized procedure. About simultaneously (1943), however, he gives a more limited definition, describing diplospory as the formation of unreduced gametophytes from embryo-sac mother-cells. Practically, GUSTAFSSON calls (just as EDMAN did previously) diplospory those processes which I have denoted as diplo-, semi- and generative apospory. When combining this practice with his definitions, the archesporial cells of, for example, *Antennaria*, which directly form unreduced gametophytes, and the unreduced »dyad-cells» of, for example, *Taraxacum* should be both spores and embryo-sac mother-cells. That this definition is at least partly absurd

is immediately evident; that it is absurd in its entirety becomes obvious from the following discussion.

Recent investigations into the cytology of the apogamogones have shown (cf. especially the summary in FAGERLIND, 1944) that »the degree of meiotization» of the archesporial cells is reduced to different extents. It may be lacking completely or, cautiously expressed, be present so faintly that it cannot convert the archesporial cells into spore mother-cells. In this case, it is obviously impermissible to denote the archesporial cells as spores, since they are gametophyte initials. They are analogous but not homologous to spores. If this analogy entitled us to regard them as spores, the gametophyte initials, when somatic apospory is present, should likewise be spores. Then, apospory should not be found at all. In apogamogones, in which the archesporial cells clearly acquire the character of spore mother-cells, where they undergo semi-heterotypic division independent of whether it is followed by the formation of restitution nuclei, the resulting cells can obviously not be denied the character of spores. As soon as the formation of restitution nuclei has occurred, these spores are diploid. *Thus, the discussion shows that my application of the terms diplospory and generative apospory corresponds to the original intention. Consequently, my limitation of their meaning is in fact only apparent.* There occurs a well-defined intermediary state between the two phenomena. In certain cases, »the degree of meiotization» may be too low to permit semi-heterotypical division, too high to suppress meiosis completely. There, we meet with the characteristic division which has been described by GUSTAFSSON under the term of pseudo-homeotypic division. Since we still feel very uncertain in our endeavours to decide whether resulting daughter-cells have or lack the character of spores — whether we are concerned with diplospory or generative apospory — I introduced the term semi-apospory in 1940. The term in itself denotes an intermediary phenomenon.

EDMAN (1931) actually considered an embryo-sac initial as homologous to a spore in those cases where, according to my terminology, we are dealing with generative apospory, and he points out: »Diese Abkürzung der Entwicklung von der Sporenmutterzelle bis zu dem Gametophyten ist indessen für die apomeiotischen Pflanzen nichts eigenartiges; sie findet auch bei den meiotischen statt, und zwar bei den *Lilium-*, *Plumbagella-* etc. Typen». This view, however, cannot be held any longer. We still find nuclei of spores in the types mentioned. They are distinguished only from the normal type by the fact that in

consequence of a lacking wall formation more than one spore-nucleus is to be found in a single coenomacrospore. If generative apospory is present, the lacking wall formation is quite another thing (FAGERLIND, 1940 a, 1944).

When GUSTAFSSON is denoting what I call generative apospory as diplospory it may be the last reminescence of previous misinterpretations. Earlier, he denied that archesporial cells in this case are submitted to somatic division. In recent years, however, he has — obviously under the influence of BERGMAN — gradually shown signs of a change of mind. Now — yet without letting it be known explicitly — he has completely or almost completely adopted the correct conception.

After having criticized »my» terms apomixis, agamogony, and diplospory, GUSTAFSSON continues: »FAGERLIND's terminology is inappropriate in several other respects», and he illustrates this by three examples. The first example is *Archieracium*, being described three times, *viz.* (1) avoiding »apomixis terms», (2) applying »my» terms, and (3) employing the terminology recommended by GUSTAFSSON. In the last description, which owing to an unfavourable fate is incomplete, some periphrases had to be made on account of lacking terms. Subsequently, GUSTAFSSON challenges to a dispute about trifles when asking which of the two last descriptions is the more adequate; both of them expressing exactly the same with respect to the apomixis phenomenon. With application of my terminology the definition can be made shorter than when using his description No. 2. Moreover, if expressed correctly, it should read as follows: *Archieracie*-biotypes have a different frequency of apogamogony connected with generative apospory (most frequently) and diplospory. Semi-apospory and somatic apospory are also said to occur.

In his second example, GUSTAFSSON points out that my terminology becomes inapplicable in those cases in which the presence of apogamogony is known; the details of its course, however, are but partially known. Moreover, if it is proved that somatic apospory is not present, the phenomenon can be denoted as diplospory under »GUSTAFSSON's terminology». With my terminology, however, there would be no possibility of denoting it. Is it actually indispensable that a terminology be applied also in cases where our knowledge is but fragmentary? As a matter of fact, if we say — and this is what GUSTAFSSON himself actually does — that diplospory, semispory or generative apospory is present, the phenomenon can be described in my terms. At any rate, GUSTAFSSON does not illustrate it more precisely by calling it »diplo-

spory». If there is a want of collective terms, they can easily be created.

The application of my terminology provides us with numerous advantages. I abstain from citing them, as they have already been enumerated (FAGERLIND, 1940 a, 1944).

GUSTAFSSON reproaches me for having completely ignored HARTMANN and his collaborators in my discussion. In the discussion of 1940, terms from his works and from a great many other papers are not considered. I felt neither induced to deal with a multitude of terms which had appeared and disappeared again nor to go into all variations concerning the application of one and the same term. I never intended to describe the historical development of the apomixis terminology, but to arrange logically the different phenomena and to give them names. The first task is naturally the more important one. Designations are less significant, although agreement on this point is most desirable. Before my abstract came out, many scientists, and GUSTAFSSON among them, worked with less logically founded classifications (terms which refer to the formation of sporophytes were applied, for example, to the whole course of formation of gametophytes, development of gametophytes, and formation of sporophytes). In his work of 1939, he tended to a more logical treatment. In the meantime, I could ascertain that GUSTAFSSON and myself are now applying the same fundamental classification of the apomictic phenomena, although one of his »partitions» has been divided into three by the present writer. My paper of 1940 has obviously already been fruitful. That GUSTAFSSON by means of polemics concerning the name of the »partition» conceals his change of mind is quite another thing.

GUSTAFSSON terminates his critical revision with a schematic review of various reproduction methods. Here (1944, pp. 149—150), apogamety connected with apo- or diplo-spory is inserted as a subdivision to the case »the reproduction is still by gametes». Finally, a little question: For what kind of ferns has the presence of the D-scheme been proved? If the conditions of *Lastræa pseudo-mas* are meant, the foundation must be taken as seriously weak.

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STUDIES ON A PECULIAR CHROMOSOME CONFIGURATION IN GODETIA WHITNEYI

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At first metaphase of meiosis *Godetia Whitneyi* shows rather many different chromosome configurations (HÅKANSSON, 1942). Rings are common. These are quite like those in *Oenothera* in only having terminal chiasmata and in consequence of this their chromosomes regularly have a zigzag orientation. It has even been shown that some *Whitneyi* types are constant structural heterozygotes: all plants have a ring, none are segregated with normal pairing (7 II). In *G. Whitneyi* there have also been found configurations of which no counterpart has been seen in *Oenothera*, e. g. monosomics with $4_0 + 4_{II} + I$, which will be discussed in another paper, and disomics with chain-of-three + $+ 5_{II} + I$.

The peculiar chain-of-three + I configuration was first observed in *G. parviflora* (HÅKANSSON, 1941), and was afterwards found in several plants belonging to the so-called *Willamette* race from North Oregon of *G. Whitneyi* (HÅKANSSON, 1942; HIORTH, 1942). This race had plants with normal pairing, with one or two rings-of-four, and with the chain-of-three + I configuration instead of the one ring. In the chain the end-chromosomes were invariably directed towards one pole, the central chromosome towards the other (like a V). The univalent lay in the equatorial plate; it lagged during first anaphase, so that in most of the PMCs it did not come into the two interkinesis nuclei (was eliminated). In view of this strong elimination it seemed peculiar that plants with a univalent were so common. Respecting the nature of this chromosome configuration, only conjectures could be formed, the most likely one being that one of the chromosomes in a ring-of-four had undergone some kind of change so that it could no longer undergo normal pairing, but appeared as a univalent.

It has not been possible to carry out further investigations of the *Willamette* race. However, two peculiar segregation phenomena studied by HIORTH in plants from Occidental, 12 miles west of Santa Rosa, Sonoma Co., and Tocaloma, Marin Co., California, proved to be associated with the chain-of-three + I configuration. These have reference

to a recessive, very sterile dwarf type, Occ.-zw_1, and a dominant cotyledon marking, Toc.-C^{pc}. Especially the former has been rather closely studied by me. Some hybrid plants with the genotypical constitution C^{pc}/zw_1 have also been subjected to a cytological analysis. Some genetical data concerning the material have been communicated to me in a letter from Dr. HIORTH, part of which I am submitting here.

DWARF TYPE FROM OCCIDENTAL.

Dwarf plants zw_1zw_1 are recognized at an early stage because they have very small cotyledons. As a rule, they arise from Occidental plants having a dominant cotyledon marking C^s; but they have also issued from plants without this marking. C^s and Zw_1 show absolute linkage. Hence the heterozygote is $C^s\ Zw_1/c\ zw_1$, the dwarf is $c\ zw_1/c\ zw_1$. Now, the peculiar feature is that the dwarf type segregates in great excess. In one case selfing of the heterozygote gave 72 normal : 40 dwarfs, and the F_2 of $zw_1zw_1 \times$ Bremen showed the segregation ratio 66 normal : 46 dwarfs. Back-crossings of the heterozygote with the normal type revealed the fact that 68 per cent. of the pollen-cells and no fewer than 87 per cent. of the functioning egg-cells had been zw_1.

The following material has been cytologically examined:

No. 1. S 3—1940. Progeny of the self-fertilized heterozygote $C^s\ Zw_1/c\ zw_1$. Here six plants with normal appearance had 5 II + chain-of-three + I. Four dwarf plants had strong asyndesis (most frequent configuration: 1 II + 12 I). Two dwarfish, richly ramified plants had 7 II.

No. 2. S 310—1942. Dwarf plants from (Occ.-$zw_1 \times$ Bremen) F_2. Stages too old. Diakinesis in ovule showed 1 II + 12 I (Fig. 12).

No. 3. 1940—331/8 s. Dwarf plants out of (Occ.-$zw_1 \times$ Bremen) F_2. Two plants showed a very strong asyndesis. In other plants meiotic stages were absent, but asyndesis could be inferred from the appearance of the pollen sporads.

Nos. 4—5. S 312—1942 and 1939—1002/1026 × 1112/801 sister families, Occ.-$zw_1 \times$ Bremen F_1. Altogether five plants showed 5 II + + chain-of-three + I.

No. 6. S 252—1943. Probably a zw_1 heterozygote out of (Occ.-$zw_1 \times$ Bremen) $\times\ C^s$. Two plants had 5 II + chain-of-three + I.

No. 7. S 235—1943. C^sC^s from $C^s \times$ Bremen S_2. Two plants had 7 II.

It is not easy to obtain meiotic stages of the dwarf type — the buds are few in number, and so are the PMCs in the loculi of the anthers.

Nos. 1, 3 and 5 have grown at Svalöf, and I am indebted to Miss MAGNA PALM of the Chromosome Laboratory for the fixing of the buds at the right stages of No. 1.

The fact that the hybrid of the dwarf with Bremen has chain-of-three + I (Nos. 4 and 5) is of special interest, since Bremen has the standard complex (see HÅKANSSON, 1942). This configuration is also presented by the other examined zw_1 heterozygotes (Nos. 1 and 6). Hence they must also contain the standard complex, which in this paper is designated *a*. The second (7-chromosome) complex of the heterozygotes may be provisionally denoted as *d'*. Thus, $C^s\ Zw_1/c\ zw_1$ is *ad'*, $c\ zw_1/c\ zw_1$ is *d'd''*, and the plants with normal pairing in Nos. 1 and 7 are *aa*.

Cytology of the zw_1 heterozygote ad'. — The chain has a V-shaped orientation at first metaphase. There is always a distinct difference in size between its end-chromosomes, one being almost one-third shorter than the other (Fig. 1). One question is, now, whether the univalent has been paired during prophase with the chain and afterwards become detached. Unfortunately, most of the *Whitneyi* types have extremely unclear diakinesis, the earlier stages being still more indistinct. This is unlike other *Godetia* species. The fact is that several cases are known of asyndesis in which this phenomenon does not appear until the end of diakinesis, normal pairing being the rule before (see PRAKKEN, 1943). The same behaviour seemed to prevail here. Certainly it could not be established by observations at diakinesis, but very often the univalent lay alongside an end-chromosome as if it had come loose from a chain-of-four, or between and above the end-chromosomes as though detached from a ring-of-four (Fig. 14). Further, plates were observed in which the univalent lay in the centre, the bivalents and chain at the periphery (Fig. 2); if the univalent had been free when the plate was formed it ought to have been on the outer side of the other chromosomes and not on the inner side. These observations could be best made in S 252. In this number (as well as in S 489) I was also able to find some PMCs in which the univalent was joined to the chain (Fig. 3). Both ring and chain-of-four chromosomes seemed to be able to occur (Figs. 4—6), although only in a few per cent. of the PMCs. In rare cases, thus, the connection can persist from prophase. As prophase cannot be studied, it is not possible to settle whether a ring is formed in prophase in all the PMCs or only in part of them.

At first anaphase the chain behaves as follows. Its end-chromosomes pass to the same pole. The univalent lags and is eliminated in

about 70 per cent. of the PMCs (Fig. 7). Rather rarely it undergoes division during first anaphase, though as a rule this division does not take place until second anaphase. There is no elimination in about 30 per cent. of the PMCs; in these PMCs the chromosome distribution may be 7 + 7 or (more rarely) 8 + 6 (Fig. 8). Hence four kinds of gones are formed: 7-chromosomal with the end-chromosomes of the chain, 7-chromosomal with the central chromosome and the univalent, 6-chromosomal, 8-chromosomal. Of these, the 6- and 7-chromosomal with end-chromosomes are the commonest. The plants examined are too few to decide whether the 8-chromosomal are viable, but the 6-chromosomal are doubtless lethal, as otherwise monosomics ought to have been formed in great number.

Cytology of aa. — 7 II (Fig. 9). Rarely, a weak asyndesis that gave rise to 2 I in No. 7.

Cytology of dwarf type (*d'd'*). — A very strong asyndesis present here.

The strongest asyndesis encountered amongst *Whitneyi* was in a 13-chromosomal and completely sterile type. Bivalents were never observed in this type, while in a nullisomic type a bivalent was found in a number of PMCs (HÅKANSSON, 1943). In a couple of anthers in a specimen from the dwarf type counts showed 14 I in 2 PMCs, 1 II + 12 I in 12 PMCs (Fig. 10), 2 II + 10 I in 3 PMCs (Fig. 11), finally, 3 II + + 8 I in 3 PMCs. Other specimens showed a higher proportion of PMCs with 2 II than these, but it is evident that 1 II is the commonest configuration, followed in order of frequency by 2 II. At most 4 II were observed. Sometimes transitional types to asyndesis are seen in the form of bivalents, whose homologues lie obliquely in the plate or are without clear connection. This suggests a higher frequency of pairing in earlier stages than in first metaphase. Finally, it may be mentioned that asyndesis has also been found in the ovules (Fig. 12).

The univalents arrange themselves into a more or less regular plate. First anaphase resembles that in the nullisomic. Sometimes two interkinesis nuclei of equal size are formed, but mostly there is a strong spread of univalents, leading to the formation of several small nuclei from one or two chromosomes. A restitution nucleus may be formed, though probably more seldom than in the nullisomic. During second anaphase all interkinesis nuclei are divided. The pollen sporads will therefore often contain several supernumerary cells. Dyads are not infrequently observed. The pollen is very irregular, with many sterile

grains. 4-lobed grains, evidently coming from dyads, are not uncommon.

Conclusions. — Theoretically, the course of meiosis in plants with chain-of-three + I is such that the chromosome number of the progeny

Figs. 1—8. Occidental-zw_1, heterozygote (*ad'*). — Figs. 3—6 show very unusual configurations. — Fig. 1: 5 II + chain-of-three + I. — Fig. 2: metaphase 1, polar view. 5 II + chain-of-three + I. — Fig. 3: 5 II + chain-of-four. — Figs. 4 and 5: chains. — Fig. 6: ring. — Fig. 7: early metaphase 2. — Fig. 8: anaphase 1, 6 + 8 chromosomes. — Fig. 9, *aa* segregated from *ad'*: 7 II. — Figs. 10—12, the dwarf zw_1zw_1 (*d'd'*) segregated from *ad'*. — Fig. 10: 1 II + 12 I. — Fig. 11: 2 II + 10 I. — Fig. 12: embryo-sac mother cell, 1 II + 12 I.

would be expected to vary from 12 to 16, but all the plants examined had 14 chromosomes. 6-chromosomal gones are here certainly sterile, while nothing is known as to the vitality of the 8-chromosomal. Presumably, however, an analysis of a larger material would lead to the discovery of »trisomics». An important question is which of the two 7-chromosomal gones is *d'*. The first assumption to suggest itself was that the chromosome represented by the univalent had undergone such alteration that it showed asyndesis as against its neighbours in the ring-of-four, the fact being that the constant appearance of a chain with its end-chromosomes of invariably unequal size pointed definitely to the same chromosome always being the univalent. Thus, the univalent and the central chromosome of the chain-of-three were thought to belong to the new *d'* complex. The genetic results, however, put another complexion on the matter. The dwarf type appears in great excess, whereas the 7-chromosomal type of gone that has the end-chromosomes of the chain is by far the more numerous. The percentage of elimination seems to correspond to the frequency of zw_1 in the pollen of the heterozygote. Accordingly, the condition of things is that the end-chromosomes in a chain belong to *d'*, while the univalent and central chromosome are *a* chromosomes.

It is assumed — using numerical denotation for the chromosome-ends — that the original chromosomes have been 1.2 and 3.4, and those altered by segmental interchange 1.4 and 2.3. These should therefore form a normal ring-of-four: 1.2—2.3—3.4—4.1. At two points an alteration has occurred that has led to the dissolution of chiasmata that had formed. If the ends responsible for this are denoted as 4' and 3', the arrangement will be the chain-of-three: '4.1—1.2—2.3' and the univalent 3.4. The *a* chromosomes are unchanged; the locus of zw_1 is in either 1.4' or 2.3', of C^s in the central chromosome or in 3.4.

Since the one structurally homozygous combination is an asyndetic dwarf, we have here an initial stage of that balanced lethality which is so common in *Oenothera*. In cross No. 1, however, the two plants with 7 II were also dwarfish though partially of a different type. According to HIORTH, these dwarf plants were undoubtedly a modification due to late sowing and of no significance in this connection.

COTYLEDON MARKING C^{pc} OUT OF TOCALOMA.

A few data concerning the genetics of Toc.-C^{pc} may be cited from a letter received from Dr. HIORTH. Inbred lines of C^{pc} exhibit an

especially strong cotyledon marking, but they segregate yellow, lethal plants without distinct marking. Three F_3 families gave, for instance, 369 normal C^{pc} : 51 yellow. HIORTH thinks that balanced lethality may come into question here.

($C^{pc} \times$ Bremen) F_2 also showed an immense excess of C^{pc} plants. Three families gave 473 C^{pc} : 24 c : 13 yellow (Bremen is cc). The back-cross $C^{pc}c \times cc$, finally yielded 991 $C^{pc}c$: 58 cc in three families. Hence the excess of C^{pc} among the functioning gones of the heterozygote is also very great here.

The cytologically examined material is here not so large.

No. 1. S 117—1942. Toc.-C^{pc}, S_2. Three plants showed 5 II + + chain-of-three + I, one of these (G 3224) showing a pronounced asyndesis.

No. 2. S 478—1943. C^{pc} plants out of (Toc.-$C^{pc} \times$ Bremen) F_2. Three examined plants had 5 II + chain-of-three + I. Fixed plants were considered to be possible homozygotes, which was thus not the case.

No. 3. S 486—1943. C^{pc} from (Toc.-$C^{pc} \times$ Bremen) $\times$ Bremen. One plant had 5 II + chain-of-three + I, one plant (G 783) had 15 chromosomes with the configuration 6 II + chain-of-three. The segregation ratio had here been 359 C^{pc} : 22 c.

Cytology of disomic C^{pc}. — The chain-of-three in C^{pc} has a different appearance from that in the zw_1 heterozygote, the two end-chromosomes being always of equal length. Their length corresponds with that of the longer end-chromosome in the zw_1 heterozygote (Fig. 13). It is clear that they have arms of very unequal length. The position of the univalent in relation to the end-chromosomes of the chain was sometimes such as to suggest ring formation in the preceding prophase (Fig. 14). Probably, the univalent was attached to the chain more rarely than in the zw_1 heterozygote.

It is quite obvious that the univalent here is eliminated still more frequently than in the zw_1 heterozygote. About 90 per cent. of the PMCs showed an eliminated chromosome during second division. As a rule, the centromere of the univalent was not divided until second anaphase. It might happen that its centromere did not divide at all. In that case the PMCs got four tetrad nuclei and one chromosome.

One plant showed great asyndesis. This asyndesis, however, was unlike that in zw_1zw_1, for the univalents did not arrange themselves in the equatorial plate but lay on either side of this as homologues in bivalents (Fig. 15). It is, accordingly, a question of a late dissolution

of bivalent chiasmata. The number of univalents was often 7—9. The material was not large, but a chain was occasionally observed, and thus the typical configuration here is also chain-of-three + I.

Cytology of »trisomic» C^{pc}. — The chain-of-three was exactly like that in other C^{pc} plants (Fig. 16). The constancy of this formation is remarkable. It is hardly ever seen divided into bivalent and univalent, whereas this division is common when ordinary trivalents are concerned. In the latter, as is known, three chromosome ends are often joined. Now and then asyndesis was observed in one of the bivalents. First anaphase is regular, with the chromosome distribution 8 + 7. Elimination never occurs or is rare.

Conclusions. — The same reasoning as in the case of Occ.-zw_1 leads to the conclusion that C^{pc} is located in one of the end-chromosomes of the chain. The excess of C^{pc} plants is here very large. The univalent elimination is, as seen, also considerably greater, but whether this alone accounts for the great excess in the cross $C^{pc} \times cc$ cannot be decided. Possibly other factors are also operative. If we denote the altered complex here as *d*", the heterozygote is *ad*". Unlike the preceding case, it has not been possible here to detect any homozygotes (*aa* and *d*"*d*"). The probability is that it is not possible to do so cytologically, maybe no such homozygotes reach the meiotic stage. Possibly the yellow, lethal plants represent one of the »homozygotes», namely *d*"*d*". HIORTH considers, it should be remembered, that balanced lethality comes into question here. However, he has not yet completely clarified the genetic conditions.

The 15-chromosomal plant G 783 has the chromosome pairing that would be expected if it has been formed from an 8-chromosomal *d*" gone and *a*. Another »trisomic» is conceivably formed from an 8-chromosomal gone and *d*". It must, however, have had quite a different chromosome pairing. The absence of asyndesis in the »trisomic» found here is of interest. One of the bivalents must be formed from the two chromosomes 3.4 (if it is this that is the I in C^{pc}), and the fact that they have paired with each other lends support to the interpretation that the univalent is an ordinary *a* chromosome.

One of HIORTH's back-crosses gave an unexpected result. $C^{pc}\,C^{s} \times cc$ generally gives a small number of C^{s} plants, e. g. in one case 9 $C^{pc}\,C^{s}\,c$: 92 $C^{pc}\,c$: 15 $C^{s}\,c$. This result is natural if C^{s} lies in the univalent 3.4, which is often eliminated. One family, however, gave 37 C^{s} : 29 $C^{pc}\,c$. As HIORTH points out in his letter, this is explicable if C^{s} in the mother plant had lain in a bivalent, that is to say, at this cross

a »trisomic» C^{pc} had been used, thus a plant with the same configuration as G 783.

The enormous elimination of univalents and the balanced lethality make C^{pc} constant. In the back-cross $C^{pc}\ c \times cc$, the results of which have been submitted above, zygotic lethal factors have not been active. The elimination, however, is probably sufficiently large to explain the small number of *cc* plants; it was 90 per cent. in the PMCs, and probably higher in the ovules.

THE HYBRID HOMOZYGOTE Toc.-d''/Occ.-d'.

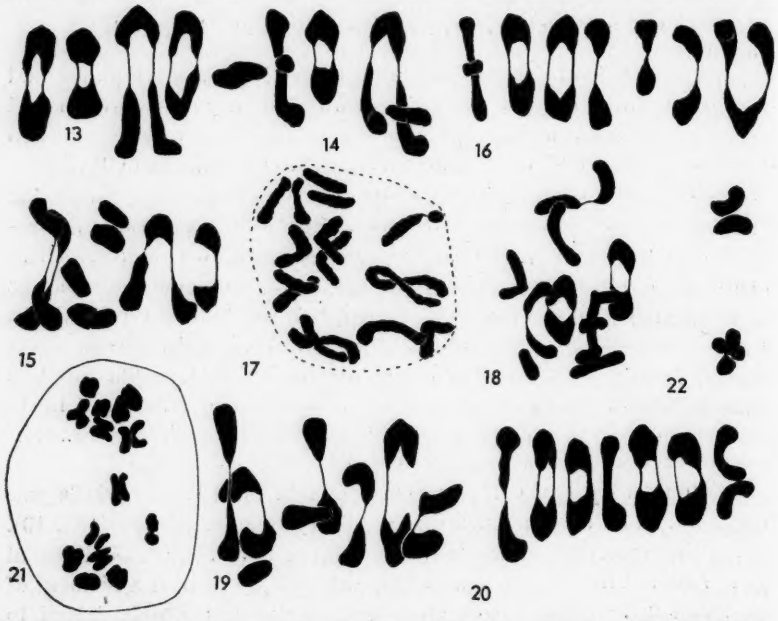
S 489—1943 consisted of the cross $C^{s}/zw_1 \times C^{pc}$. Five plants had been fixed which *might* be C^{pc}/zw_1. Two of them had chain + I and will therefore not come into question here. The other three all showed the same pairing and were clearly *d'd''*. An examination of this combination ought to clarify the question as to whether they were the same chromosomes as formed the chain in C^{pc} and in the dwarf heterozygote. If they were quite different chromosomes, two chains and two univalents would be expected. If they were the same chromosomes as formed the chains, the most likely expectation would be seven bivalents. If two *d* chromosomes were alike but two unlike, i. e. if the same chromosome had been involved in the segmental interchange but this had taken place in both cases with different chromosomes, the most likely expectation would be a chain-of-three (and probably 3 I). However, none of these configurations occurred.

Cytology. — The configuration found in most of the PMCs was 6 II + 2 I. The two univalents were clearly of unequal size (Fig. 19). When there were only two univalents, these were always of different size. I do not believe I saw any PMC where they formed a bivalent of the usual appearance. Now and then they were certainly joined to each other, but it is doubtful whether this had taken place by chiasmata (Fig. 20). In any case it seems too risky to draw any conclusions from the appearance of this formation as to the structure of these chromosomes.

Often there occur another two univalents, these showing no difference in size (Fig. 18). It is about 30 per cent. of the PMCs that show the 5 II + 4 I configuration. More univalents do not occur. It thus seems as if the two new univalents were due to asyndesis in a definite bivalent. In some PMCs the chromosome configuration could be

determined in diakinesis and early first metaphase (Figs. 17 and 18). The univalents were also present here.

The first anaphase becomes very irregular on account of the univalents being retarded and eliminated in a very high percentage. Fig. 21 shows a late first anaphase with two lagging univalents of different size. At one pole are seen seven chromosomes, at the other five. As a matter of fact, a non-disjunction seems to be relatively common, and is presumably caused by two univalents passing to the same pole. During second division eliminated chromosomes are seen in



Figs. 13—16. Tocaloma-C^{pc}. Figs. 13—15 *ad*", Fig. 16 *ad*" + I. — Fig. 13: 5 II + + chain-of-three + I. — Fig. 14: chain-of-three + I. — Fig. 15, 3 II + chain-of-three + 5 I. — Fig. 16: 6 II + chain-of-three. — Figs. 17—22, Occ.-zw_1/Toc.-C^{pc}(*d'd*"). — Fig. 17: diakinesis, 5 II + 4 I. — Fig. 18: early metaphase 1, 5 II + 4 I. — Fig. 19: metaphase 1, 6 II + 2 I. — Fig. 20: 6 II and »pseudobivalent». — Fig. 21: anaphase 1, 7 + 5 and 2 eliminated chromosomes. — Fig. 22: eliminated I:s from a PMC in interkinesis.

practically every PMC. The sporads consequently have supernumerary pollen-cells. There should be a very considerable pollen sterility.

Conclusions. — The absence of a chain in this hybrid homozygote would seem to show that the same chromosomes are involved as form the chain-of-three + I in the two heterozygotes. Remarkably enough,

however, the pairing was not 7 II. Asyndesis is present in some bivalents. The difference in size of the two constant univalents must be due to the fact that one of them is the short end-chromosome in the *Occidental* chain, the other corresponding to an end-chromosome from C^{pc}. It is therefore probable that the two new univalents found in 30 per cent. of the PMCs represent the other end-chromosome from the respective chains. This asyndesis is however surprising. In $C^{pc} \times$ Bremen and $zw_1 \times$ Bremen these chromosomes are paired with the same central chromosome 1.2, and ought therefore to be paired with each other.

Perhaps the situation is that although the same chromosomes take part in the chain + I configuration in the two heterozygotes, the central chromosome of the chain and the univalent are not the same. In the zw_1 heterozygote 1.2 may be the univalent, in the C^{pc} 3.4. The former then has the configuration '2.3—3.4—4.1' + 1.2, the latter '4.1—1.2—2.3' + 3.4. Toc.-C^{pc}/Occ.-zw_1 gets the four chromosomes 1.4', '1.4, 2.3', '2.3. It is clear that these have difficulty in forming two bivalents, especially the ones showing a size difference. However, the assumption that in the C^{pc} a different *a* chromosome is the univalent than in the zw_1 heterozygote should be subjected to genetical tests. C^s has been assumed to be located in the *a* chromosome 3.4. In the C^{pc} this chromosome seems to be the univalent. In $C^s\ Zw_1/c\ zw_1$, thus, C^s would be in the central chromosome of the chain. It ought to be possible to settle whether this is the case.

GENERAL.

The continued investigations of the chain-of-three + I configuration have considerably increased our knowledge of it, but its real nature is still unelucidated. Results from the genetical investigations will soon be published by Dr. HIORTH. An advance report has already been given by him (1944).

It is now fairly evident that in prophase the four chromosomes can form an ordinary ring. When the equatorial plate has been completely formed, one chromosome has always become detached from the ring. It often lies near the chain, though it is often found further away, in which latter case it has probably become detached earlier, or maybe has not been paired at all. That it is a definite chromosome which detaches from the ring is evident from the fact that the chain in the zw_1 heterozygote always has one smaller and one larger end-chromosome. Hence it is here a question of an asyndesis that always affects the same chromosome.

A remarkable fact is that what entails the asyndesis of this chromosome is not present in it but in the end-chromosomes of the chain, the asyndetic chromosome being an ordinary *a* chromosome. This is quite evident from the genetical tests: *aa* is formed in great deficiency, and therefore the so often eliminated univalent must belong to this complex. Other evidence is that a 15-chromosomal plant had 6 II + + chain, which shows that the chromosome which is the univalent can form an ordinary bivalent.

There were certain cytological differences between Toc.-C^{pc} and zw_1. In the former the end-chromosomes of the chain were equally long, in the latter there was a distinct difference. At anaphase the behaviour of the chain is almost always such that the central chromosome passes to one pole, the end-chromosomes to the other. There is also a difference in the behaviour of the univalent during anaphase. It is often eliminated. In the zw_1 heterozygote the elimination is about 70 per cent., in the C^{pc} it is certainly at least 90 per cent. The different elimination probably brings about a difference in the genetics of the two types, for in the crosses a higher percentage of C^{pc} than of zw_1 functions in the respective heterozygotes.

There is a great difference between the two examined types with chain-of-three + I. If the standard complex is denoted by *a* and the altered complex by *d'* and *d''* respectively, we get the formula *ad'* for the Occidental type and *ad''* for the Toc.-C^{pc}. *ad'* segregates the two structural homozygotes *aa* and *d'd'*. Of these, however, *d'd'* has a much reduced vitality, is a dwarf with strong asyndesis, and occurs in excess. *ad''* segregates no structurally homozygous combinations so far as is known at present. There arises, however, a number of yellow plants that may be *d''d''*, though this latter fact cannot be cytologically verified on account of their lethality. It appears as if C^{pc} has a balanced lethality like that in many *Oenotheras*, though attached to a chain + I instead of a ring. This configuration undoubtedly suffers from the drawback that gones with different chromosome numbers are formed, which is wastefulness. Those with six chromosomes are not vital. On the other hand, a »trisomic» C^{pc} plant shows that a 8-chromosomal gone is vital.

Thus, the chain + I configuration is really a ring-of-four where asyndesis has fallen on a definite chromosome. The study of chromosome pairing in the combination *d'd''* showed that it was the same chromosomes which had formed the ring in the two cases. It also seemed to show that it was not the same *a* chromosome which formed the univalent in *ad'* as in *ad''*. The difference in the appearance of the chains

is presumably due to the segmental exchange having taken place differently in the two cases. Thus, the chains have probably arisen independently of each other. The chain observed in the *Willamette* race (HÅKANSSON, 1942) is like that in Occ.-zw_1.

Now that the univalent has proved to be an ordinary *a* chromosome, its frequent occurrence in nature despite the elimination is no longer remarkable. It is, of course, by no means irreplaceable.

There have been discovered different kinds of »heterozygotic» chromosome configurations which are more or less constant in that they are to be found in all or a great number of the individuals occurring in nature of the type in question. Here belong the inert or semi-inert supernumerary chromosomes in maize, rye, or *Sorghum*. Generally their number is not quite constant, and they are often unpaired at meiosis. Such chromosomes have been found by me in *Godetia*, though not in the *Whitneyi* species. Another kind of heterozygote is encountered in the *canina* forms of *Rosa*. This form manifests itself in a definite number of bivalents and univalents; heterogamy, »internal triploidy» with an inability to form trivalents, characterizes these types and gives them their constant chromosome configuration (see GUSTAFSSON and HÅKANSSON, 1942). Then there are the well-known *Oenothera* rings, constant as a consequence of the lethal nature of the structurally homozygotic combinations or from other causes. There are several examples of such constant rings in *Godetia Whitneyi*.

Chain-of-three + 1 is a structurally heterozygotic configuration that is unknown outside *Godetia*. Here, a definite chromosome is always free, while the other chromosomes of the ring form a chain-of-three, the chromosomes of which are arranged as a V. The free chromosome is an unchanged *a* chromosome, a fact that has great significance for the genetics of these types. As a result of the strong univalent elimination gones with a complete *a* complex are formed in great deficiency. Here, therefore, the one homozygotic combination will be formed in great deficiency in crosses between heterozygotes and in back-crosses with races having the standard chromosomes (the latter being especially important, as *G. Whitneyi* is an allogam). Hence a rival of the new complex is immediately disposed of, without recourse to lethal genes, certation, selective fertilization, or suchlike. The price paid is great gone sterility, 6-chromosomal gones being manifestly lethal in these cases. However, as the number of ovules is very large, this sterility is not of so great importance, a sufficient number of seeds nevertheless being formed. The new structurally homozygotic combination is prob-

ably lethal in the one case, in the other case sublethal in the form of a very pronounced dwarf with very strong asyndesis and considerable sterility. A sublethal type of this kind has previously been discovered in *G. Whitneyi*, it is segregated by plants from Corvallis, Oregon. It is called »verkrüppelt» (stunted) and it, too, constituted the homozygotic realization of a new changed complex. Here, however, the structural heterozygote had a ring-of-six (HÅKANSSON, 1942), and the structural homozygote had 7 II and did not show asyndesis. Structural homozygotes that are dwarfs are also known in *Oenothera*. *Oe. pratincola*, which has a large chromosome ring, segregates a dwarf type with 7 II, a process that was first improperly called »mass-mutation» (see RENNER, 1942). OEHLKERS has succeeded in obtaining some plants from the homozygotic combination *curtans-curtans*. They were very small and showed 7 II (OEHLKERS and HARTE, 1943). Thus, asyndesis does not occur among the homozygotic *Oenothera* dwarfs.

It is difficult to frame a theory that satisfactorily accounts for the pairing conditions described in this paper, i. e. not only chain + I in *ad*' and *ad*" but also the asyndesis in *d*'*d*' and *d*'*d*". In *d*'*d*" there were always found at least two, though not more than four univalents. So simple an explanation as that the centromere in the end-chromosomes is closer to the free end does not suffice. Certainly in *Whitneyi* a long chromosome with a subterminal centromere at first metaphase is as a rule without a chiasma in the short arm, but, in the first place, the bivalent formed by these chromosomes is not always open and, in the second place, the asyndesis in *d*'*d*' remains unexplained. It also seems improbable that the asyndesis is governed by a gene. The fact that pairing occurs at least sometimes during prophase but is afterwards followed by dissociation certainly directs attention to the above-mentioned asyndetic rye. Here, however, it must in that case be a dominant gene, and this cannot lie in the chromosome which is the univalent but in the chain, and it must influence chiasma formation in two definite chromosome-ends belonging to different chromosomes. A pleiotropic and at the same time specific gene action of this type appears to be improbable.

Instead of this, the working hypothesis employed in this paper has been that it is certain properties in the chromosome-ends 4' and 3' which cause the chiasmata formed there to break before first metaphase, with the result that a chromosome having completely normal pairing properties is always the univalent. This hypothesis meets with difficulties when applied to the pairing in *d*'*d*", but, if the situation is such that

another chromosome is the univalent in *ad'* than in *ad''*, then these difficulties will scarcely present themselves (see above).

HIORTH (1944) suggests two alternatives in explanation of this configuration. Alternative I presumes a hybrid between a race with 7 II and standard chromosomes and a race with 7 II but with two of these formed by the chromosomes 1.4' and 2.3' respectively, which bivalents are always open because the ends marked ' cannot conjugate. He finds it difficult to account for the pairing in *d'd'*, which of course ought to be 7 II, two of them open, and *d'd''* is likewise difficult to explain. Alternative II presupposes that the chromosome-ends 4' and 3' are able to pair with identical ends, i. e. 4' or 3', but not with 3 or 4. It is some kind of structural alteration that 3' and 4' have undergone which renders such pairing impossible. In this case constantly open bivalents ought not to occur in the homozygote, but ordinary such. The first alternative is considered by HIORTH to be much the more probable one, but the asyndesis in *d'd'* is more suggestive of a structural change involving deficiency in the *d'* complex.

SUMMARY.

Some *Godetia Whitneyi* plants from Occidental, Sonoma Co., California, segregate a recessive, strongly sterile dwarf type zw_1zw_1. Zw_1zw_1 is a structural heterozygote with the peculiar chromosome configuration 5 II + chain-of-three + I. The chain is like a V with end-chromosomes of different size. The univalent is eliminated in 70 per cent. of the PMCs. zw_1zw_1 shows strong asyndesis with most frequently 1 II + 12 I. The heterozygote also segregates plants with 7 II.

The standard complex in *G. Whitneyi* is denoted *a*, the complex of the dwarf type *d'*. The heterozygote is *ad'*, plants with 7 II *aa*, the dwarf type *d'd'*. The last-mentioned is formed in great excess. The univalent and the central chromosome of the chain belong to *a*, the end-chromosomes to *d'*.

Some plants from Tocaloma, Marin Co., California, with a dominant marking on the cotyledons, C^{pc}, also have 5 II + chain-of-three + I. Here, the end-chromosomes of the chain are equally large and the univalent is eliminated in 90 per cent. of the PMCs. The heterozygote is here designated as *ad''*. C^{pc} is present in an end-chromosome, and here, too, the univalent and central chromosome are ordinary *a* chromosomes. *aa* and *d''d''* are probably lethal (a case of balanced lethality). One plant had 6 II + chain-of-three.

The combination *d'd''* usually had 6 II + 2 I, the latter being of different size. Often there were 5 II + 4 I. The univalents are certainly end-chromosomes of the chains. The pairing observed suggests that it is the same chromosomes which form the chain + I configuration in the two structural heterozygotes, but that another chromosome is the univalent in *ad'* than in *ad''*.

The nature and significance of the chain-of-three + I configuration is discussed.

Dr. HIORTH, Ås, Norway, has carried out the genetical investigations.

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GENSTUDIEN AN PISUM SATIVUM
VI—VIII

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(With a Summary in English)

VI. WEITERE ERGEBNISSE ZUR VERERBUNG DER WACHSLOSIGKEIT.

EINE Übersicht der bis vor kurzem bekannten genischen Grundlagen für die Ausbildung verschiedener Wachsig- bis Wachslosigkeit wurde vom Verfasser 1939 veröffentlicht. Das l. c. Angeführte kann kurz folgendermassen zusammengefasst werden:

Bl, ein Grundgen für Wachsigkeit; *bl bl*-Pflanzen sollen demnach, welche genische Konstitution sie i. ü. auch haben mögen, stets ganz wachslos sein (WHITE, 1917; WELLENSIEK, 1928 a und b). Alle verschieden schwach oder stark wachsigen Pflanzen müssen in Übereinstimmung hiermit *Bl* sein.

Wa_2—Wa_1—*wa*. Wa_2 bedingt starke, Wa_1 schwache und *wa* sehr schwache Wachsigkeit (WELLENSIEK, 1928 a und b).

Wb_2—Wb_1—*wb*. Wb_2 bedingt starke, Wb_1 zwischen starke und schwache und *wb* schwache Wachsigkeit (WELLENSIEK, 1928 a und b).

Über die Wirkung der verschiedenen Allelenkombinationen der *Wa*- und *Wb*-Serien teilt WELLENSIEK (1928 a und b) folgendes Schema mit:

Bl Wa_2 Wb_2	Stark wachsig (Haarsteegsche = Express);
Bl Wa_2 Wb_1	Wachsschwach, zwischen stark und wenig wachsig (Smaragd Reuzen, Vlijmsche Krombeck);
Bl Wa_2 *wb*	Schwach wachsig (Pois à brochettes, Chatenay);
Bl Wa_1 Wb_2	Schwach wachsig (Emereva);
Bl wa Wb_2	Sehr wenig wachsig (Sutton's Emerald Gem);
bl Wa_2 Wb_2	Ohne Wachs (Johnson's British Empire).

Wlo, ein Gen für lokal begrenzte Wachslosigkeit, das in rezessiver Form vollkommene Freiheit der Oberseite der Blättchen von Wachs bedingt, während alle übrigen Teile der Pflanze normal wachsig sind (E. NILSSON, 1933).

Wsp, ein zweites Gen für lokal begrenzte Wachslosigkeit, das vom

Verf. l. c. neubeschrieben worden ist. *wsp* hat im Vergleich mit *wlo* genau reziproke Wirkung; nur die Oberseite der Blättchen ist normal wachsig, während alle übrigen Teile der Pflanze ganz ohne Wachs sind.

Was wir in unseren Kenntnissen über die Wachsigkeit und ihre Vererbung bei *Pisum* vor allem vermissen, sind teils eine genaue vergleichende Charakteristik der Ausbildung (der Stärke) des Wachsüberzuges auf den einzelnen Pflanzenteilen, teils genanalytische Ergebnisse über das Zusammenwirken verschiedener Gene in eben genannter Hinsicht. Im folgenden sollen die Resultate einiger zur Klärung dieser Fragen ausgeführten Untersuchungen mitgeteilt werden.

DAS ZUSAMMENWIRKEN VERSCHIEDENER WACHSGENE.

Die Gene wlo und wsp. Als *wlo*-Elter wurde die von E. NILSSON (1933) entdeckte *wlo*-Linie (= meine L. Nr. 341), als *wsp*-Elter die von mir (LAMPRECHT, 1939) aufgefundene *wsp*-Linie Nr. 360 benutzt. Wie bereits erwähnt, bedingt *wlo* vollkommene Wachslosigkeit auf der Oberseite der Blättchen, *wsp* dagegen auf allen übrigen Teilen der Pflanze. Die wachsigen Teile von sowohl *wlo*- wie *wsp*-Pflanzen sind — wie gewöhnlich — stark wachsig. Gewisse Unterschiede in der Stärke der Wachsigkeit bestehen jedoch, auf die später zurückgekommen werden soll. Die Wachsigkeit bzw. die Wachslosigkeit von *wlo* und *wsp* ergänzen sich demnach insofern vollkommen, als sie die Gesamtoberfläche der Pflanze betreffen. Die lokal so scharf begrenzte Wirkung dieser beiden Gene, die sich doch auf eine Eigenschaft, die Wachsigkeit, beziehen, die man gern mit einer Funktion aller Zellen der Pflanze in Beziehung zu bringen geneigt ist, erscheint unerwartet und daher bemerkenswert. Es erschien daher auch von besonderem Interesse das Zusammenwirken dieser beiden Gene kennen zu lernen. In meiner früheren Arbeit (1939, S. 469) habe ich erwähnt, dass es einstweilen denkbar erscheint, dass *wsp* ein Allel zu *wlo* sein könnte.

Kreuzung Nr. 503, L. 341, *wlo* × L. 360, *wsp*, wird auf die oben angeführten Fragen Antwort geben. Ausser in den Genen *wlo* und *wsp* unterscheiden sich die beiden Elternlinien noch in den Genen *bt* und *pa*. *Bt—bt* entspricht dem Eigenschaftspaar stumpfes—spitzes Hülsenende, *Pa—pa* hellgrüne—dunkelgrüne Blattfarbe. Die Pflanzen der F_1-Generation waren auf allen Teilen normal stark wachsig. In F_2 wurden 200 Samen gesät und 162 vollkommen beurteilbare Pflanzen erhalten. Die vier Gene *Bt*, *Pa*, *Wlo* und *Wsp* zeigten folgende Spaltungsverhältnisse:

120 *Bt* : 42 *bt* ; D/m für 3 : 1 = 0,27
119 *Pa* : 43 *pa* ; » » » = 0,45
119 *Wlo* : 43 *wlo* ; » » » = 0,45
119 *Wsp* : 43 *wsp*; » » » = 0,45

Diese Gene spalteten demnach alle klar monohybrid. Für die Zweigenenspaltungen ergaben sich folgende Zahlen:

Gefunden: 88 *Bt Pa* : 32 *Bt pa* : 31 *bt Pa* : 11 *bt pa*
Erwartet: 91,1 » : 30,4 » : 30,4 » : 10,1 »
D/m für
9 : 3 : 3 : 1 = — 0,49 + 0,33 + 0,13 — 0,29

87 *Bt Wlo* : 33 *Bt wlo* : 32 *bt Wlo* : 10 *bt wlo*
D/m für
9 : 3 : 3 : 1 = — 0,65 + 0,53 + 0,33 — 0,04

90 *Bt Wsp* : 30 *Bt wsp* : 29 *bt Wsp* : 13 *bt wsp*
D/m für
9 : 3 : 3 : 1 = — 0,18 — 0,07 — 0,28 + 0,94

91 *Pa Wlo* : 28 *Pa wlo* : 28 *pa Wlo* : 15 *pa wlo*
D/m für
9 : 3 : 3 : 1 = — 0,02 — 0,48 — 0,48 + 1,58

85 *Pa Wsp* : 34 *Pa wsp* : 34 *pa Wsp* : 9 *pa wsp*
D/m für
9 : 3 : 3 : 1 = — 0,97 + 0,73 + 0,73 — 0,36

92 *Wlo Wsp* : 27 *Wlo wsp* : 27 *wlo Wsp* : 16 *wlo wsp*
D/m für
9 : 3 : 3 : 1 = + 0,14 — 0,68 — 0,68 + 1,91

Welche Typen von Wachsigkeit konnten nun in dieser Kreuzung unterschieden werden? Die *Wlo Wsp*-Pflanzen waren, wie schon F_1 zeigte, vollkommen normal wachsig. Die *Wlo wsp*- und die *wlo Wsp*-Pflanzen entsprachen der vorher für *wsp* bzw. *wlo* mitgeteilten Beschreibung. Und die *wlo wsp*-Pflanzen waren von allen anderen sehr leicht zu unterscheiden, indem sie auf keinem Teil auch nur eine Spur von Wachs hatten.

Vollkommen wachslose *Pisum*-Pflanzen sind in der Literatur schon früher erwähnt (WHITE, 1917 und WELLENSIEK, 1928 a und b). Bei diesen soll aber, wie schon einleitend hervorgehoben worden ist, die Wachslosigkeit durch Rezessivität in einem Grundgen *bl* bedingt werden.

Alle *bl*-Pflanzen, gleichgültig welche genotypische Konstitution sie i. ü. auch haben mögen, sollen ganz wachslos sein. Mir ist es bisher leider nicht gelungen Samen von *bl*-Pflanzen zu erhalten. In der oben besprochenen Kreuzung Nr. 503 haben wir einen genisch ganz *neuen Typus von vollkommener Wachslosigkeit* kennen gelernt, der *durch Rezessivität in den beiden Genen für partielle Wachslosigkeit, wlo und wsp, bedingt* wird. Nach unseren bisherigen Kenntnissen soll daher allen ganz wachsigen Pflanzen von *Pisum* die genotypische Konstitution *Bl Wlo Wsp* zukommen. Die Besprechung der verschiedenen Stärke des Wachsüberzuges auf den einzelnen Teilen der Pflanze soll gemeinsam mit den Ergebnissen der nächsten Kreuzung stattfinden.

Die Resultate von Kreuzung Nr. 503 zeigen ferner an, dass die vier Gene *Bt*, *Pa*, *Wlo* und *Wsp* unabhängig voneinander spalten. Die Werte für D/m zeigen durchweg gute Übereinstimmung mit dem theoretisch nach 9 : 3 : 3 : 1 erwarteten Spaltungsverhältnis an.

Die Gene wb und wlo. Das Zusammenwirken dieser beiden Gene sowie auch das der Gene *wa* und *wlo* ist schon von E. NILSSON (1933) untersucht worden. In beiden diesen Fällen konnten die F_2-Individuen auf vier Phänotypengruppen verteilt werden, die mit dem bifaktoriellen Verhältnis 9 : 3 : 3 : 1 sehr gut übereinstimmen. NILSSON veröffentlichte jedoch keine Charakteristik dieser Phänotypen.

Kreuzung Nr. 504, L. 341, *wlo* × L. 471, *wb*. Linie 471 wurde von mir aus Kreuzung Nr. 25 (L. 5 aus Chenille × L. 102 aus Acacia) erhalten. Von hier in Frage kommenden Genen ist L. 471 noch in *tl* und *s* rezessiv. *Tl—tl* entspricht dem Eigenschaftspaar: in Ranken umgewandelte Blättchen—nur Blättchen; *S—s*: nicht verklebte—miteinander verklebte reife Samen. In bezug auf *Wb* und *Wlo* siehe oben. Die F_1-Individuen wichen von beiden Eltern ab und zeigten normale Wachsigkeit. In F_2 wurden 500 Samen gesät und 465 vollkommen beurteilbare Pflanzen erhalten. Die vier Gene *Tl*, *S*, *Wb* und *Wlo* zeigten folgende Spaltungsverhältnisse:

343 *Tl*	: 122 *tl*	;	D/m	für	3 : 1	= 0,56
359 *Wb*	: 106 *wb*	;	»	»	»	= 1,10
362 *Wlo*	: 103 *wlo*	;	»	»	»	= 1,42
395 *S*	: 70 *s*	;	»	»	»	= 4,95

Von den vorstehenden vier Genpaaren spaltete nur *S* : *s* nicht klar monohybrid. Für *s*-Pflanzen besteht ein beträchtliches Defizit. Für 3 : 1 beträgt D/m — 4,95, für 15 : 1 + 7,85, wenn man einen Überschuss bzw. ein Defizit an Rezessiven mit einem + bzw. einem — bezeichnet.

Die Erklärung dieses Defizites ist, wie von mir bereits früher hervorgehoben worden ist (LAMPRECHT, 1936), darin zu suchen, dass gleichzeitig Spaltung in bezug auf den Abstand zwischen den Samen in der Hülse und eventuell auch in bezug auf Samengrösse vorkommt, was zur Folge hat, dass bei einem Teil der *s*-Individuen die Samen während des Reifeprozesses nicht miteinander in Berührung stehen und daher auch nicht miteinander verkleben können.

Für die Zweigenenspaltungen ergaben sich folgende Verhältnisse:

Gefunden:	261 *Tl Wb* : 82	*Tl wb* : 98	*tl Wb* : 24	*tl wb*
Erwartet:	261,56 » : 87,19 »	: 87,19 »	: 29,06 »	
D/m für 9 : 3 : 3 : 1	— 0,05	— 0,62	+ 1,28	— 0,97
	282 *Tl Wlo* : 61	*Tl wlo* : 80	*tl Wlo* : 42	*tl wlo*
Erwartet laut monohybr. Spaltg.	267,0 »	: 76,0 »	: 95,0 »	: 27,0
D/m für 9 : 3 : 3 : 1	+ 1,40	— 1,78	— 1,78	+ 2,78
	292 *Tl S* : 51	*Tl s* : 103	*tl S* : 19	*tl s*
Erwartet laut monohybr. Spaltg.	291,4 »	: 51,6 »	: 103,6 »	: 18,4 »
D/m für 9 : 3 : 3 : 1	+ 0,05	— 0,07	— 0,07	+ 0,11
	279 *Wb Wlo* : 80	*Wb wlo* : 83	*wb Wlo* : 23	*wb wlo*
D/m für 9 : 3 : 3 : 1	+ 1,63	— 0,85	— 0,50	— 1,16
	355 *Wb S* : 4	*Wb s* : 40	*wb S* : 66	*wb s*
Erwartet laut monohybr. Spaltg.	305,0 »	: 54,0 »	: 90,1 »	: 15,9 »
D/m für 9 : 3 : 3 : 1	+ 4,88	— 7,24	— 5,87	+ 12,78
	307 *Wlo S* : 55	*Wlo s* : 88	*wlo S* : 15	*wlo s*
Erwartet laut monohybr. Spaltg.	307,4 »	: 54,6 »	: 87,6 »	: 15,4 »
D/m für 9 : 3 : 3 : 1	+ 0,03	— 0,06	— 0,05	+ 0,06

Wie die vorstehenden Zahlen anzeigen, scheinen die Genpaare *Tl Wb*, *Tl S*, *Wb Wlo* und *Wlo S* unabhängig voneinander zu spalten. *Wb* und *S* sind zweifellos stark miteinander gekoppelt, was schon seit langem bekannt ist. Nach Korrigierung des gefundenen Spaltungsverhältnisses mit Hinblick auf das Rezessivendefizit findet man einen Crossoverprozent von nur $0{,}54 \pm 1{,}80$. Die bisher in der Literatur (s. LAMPRECHT, 1939) mitgeteilten Crossoverprozente variieren bei dieser Koppelung von 0,9 bis etwa 10. — Die für das Genpaar *Tl Wlo* gefundenen Zahlen scheinen eine schwache Koppelung anzuzeigen. Nach entsprechender Korrigierung erhält man hier einen Crossoverprozent von $37{,}4 \pm 2{,}96$. Ich betrachte diese Koppelung aber einstweilen nicht als sicher.

In bezug auf die in Kreuzung 503 und 504 gefundene sowie für das Gen *wa* untersuchte, verschieden starke Wachsigkeit bzw. Wachslosigkeit der einzelnen Pflanzenteile sei anstatt einer Beschreibung eine tabellarische Übersicht mitgeteilt. Der Grad der Wachsigkeit ist in den Rubriken von Tab. 1 durch Zahlen angegeben, wobei 1 stark wachsig,

TABELLE 1. *Die Stärke des Wachsüberzuges auf den einzelnen Pflanzenteilen verschiedener Genotypen von Pisum sativum.*

Nr.	Genotypus	Stengel	Hülsen	Nebenblätter		Blättchen	
				Obers.	Unters.	Obers.	Unters.
1	*Wa_2 Wb_2 Wlo Wsp*	1	1	1	1	1/2	1
2	*Wa_2 wb Wlo Wsp*	1/4	0	1/5	1/5	1/2—1/3	1/4—1/5
3	*wa Wb_2 Wlo Wsp*	1/3	0	0	0	1/3	0
4	*Wa_2 wb wlo Wsp*	1/4	0	1/5	1/5	0	1/4—1/5
5	*Wa_2 Wb_2 wlo Wsp*	1	1	1	1	0	1
6	*Wa_2 Wb_2 Wlo wsp*	0	0	0	0	1/2	0
7	*Wa_2 Wb_2 wlo wsp*	0	0	0	0	0	0

0 ganz ohne Wachs bedeutet. Die Bruchzahlen geben die verschiedene Stärke des Wachsüberzuges an; je mehr der Bruch sich 0 nähert, umso schwächer ist der Wachsüberzug. Die Brüche sind jedoch nicht etwa als ein direktes Mass der Dicke des Wachsüberzuges aufzufassen. Sie entsprechen nur einer Gradierung, die sich bei Übung noch mit dem Auge sicher beherrschen lässt. Bedingung ist natürlich, dass die einzelnen Typen zwecks Vergleich zugänglich sind. In bezug auf den Wachs-Phänotypus braucht der Tabelle kaum etwas hinzugefügt zu werden, sie gibt diesbezüglich vollen Bescheid.

Tabelle 1 gibt indessen ausserdem wertvolle Aufschlüsse über das

Zusammenwirken der verschiedenen Wachsgene. Vergleichen wir zuerst die Genotypen 1 und 5 miteinander, die sich nur im Gen *wlo* unterscheiden, so zeigt sich, dass die *wlo*-Pflanzen mit Ausnahme der Blättchenoberseite auf allen Teilen der Pflanze genau denselben Grad von Wachsigkeit aufweisen wie die entsprechenden *Wlo*-Pflanzen. Nur die Oberseite der Blättchen ist ganz ohne Wachs. Daraus kann geschlossen werden, dass *wlo* die Ausbildung bzw. Ausscheidung von Wachs durch die Epidermiszellen der Blättchenoberseite inhibiert, während dieses Gen auf die Bildung bzw. Ausscheidung von Wachs aller übrigen Epidermiszellen der Pflanze keinen Einfluss besitzt. Wir können uns diese Wirkung auch sehr gut so vorstellen, dass *wlo* den in den Epidermiszellen der Blättchenoberseite ablaufenden, durch andere Gene (*Bl*, *Wa* und *Wb*) bedingten Wachsbildungsprozess aufhebt oder so abändert, dass er statt zur Bildung von Wachs zu der einer anderen Substanz in den Zellen führt.

Ganz derselbe Gedankengang gilt bei einem Vergleich der Genotypen 1 und 6, die sich nur im Gen *wsp* unterscheiden. In diesem Fall inhibiert *wsp* den Wachsbildungsprozess in allen Epidermiszellen der Pflanze mit Ausnahme der der Oberseite der Blättchen. Und diese zeigt auch hier denselben Grad von Wachsigkeit wie bei den entsprechenden *Wsp*-Pflanzen. Die beiden Gene *wlo* und *wsp* haben demnach eine voneinander ganz unabhängige, lokal scharf begrenzte Wirkung auf den Wachsbildungsprozess. Und wo sie nicht wirken, führt der Wachsbildungsprozess zum gleichen Grad von Wachsausscheidung wie bei den entsprechenden *Wlo*- bzw *Wsp*-Pflanzen. Schon diese Feststellung würde das in der oben besprochenen Kreuzung Nr. 503 gefundene Ergebnis erwarten lassen, dass nämlich *wlo wsp*-Pflanzen vollkommen wachslos sind. Die Anwesenheit des rezessiven Gens *wlo* oder *wsp* scheint demnach ausserhalb ihres lokal begrenzten Wirkungsbereiches den Effekt der Wachsbildungsgene *Bl*, *Wa* und *Wb* in keiner Weise zu beeinflussen.

In noch schönerer Weise zeigt sich diese Wirkung der Inhibitoren oder Hemmungsgene *wlo* (und *wsp*), wenn sie in *wb*- (oder *wa*-)-Pflanzen auftreten. In der Tabelle 1 ist diesfalls Genotypus 2 mit 4 zu vergleichen. Rezessivität in *wb* bedingt eine auf den einzelnen Pflanzenteilen verschieden starke Verminderung des Grades der Wachsigkeit (vgl. Genotypus 1 mit 2 in der Tab.). Kommt *wlo* hinzu (Genotypus 4), so bleibt die Oberseite der Blättchen ganz ohne Wachs, während alle übrigen Teile der Pflanze den durch *wb* bedingten verschiedenen Grad

von Wachsigkeit (Genotypus 2) beibehalten. Gleiches gilt mit grösster Wahrscheinlichkeit auch für die Kombinationen mit *wsp* und *wa*.

Zusammenfassend kann die Wirkung der Wachsgene auf Grund des bisher bekannten folgendermassen definiert werden:

Bl bewirkt die Ausbildung einer Muttersubstanz für Wachs; *bl*-Pflanzen fehlt diese Muttersubstanz, weshalb sie stets vollkommen ohne Wachs sind; es kann auch mit Hilfe der Gene *Wb* und *Wa* nicht zur Bildung von Wachs kommen.

Wb_2—Wb_1—*wb* und Wa_2—Wa_1—*wa* sind zwei Allelenserien für die Ausbildung von Wachs. Jedes dieser Allele und anscheinend auch jede Kombination dieser Allele bedingt eine bestimmte Wachsigkeit der Pflanze. Dabei ist die Stärke des Wachsüberzuges, je nach der Kombination dieser Allele, auf den einzelnen Pflanzenteilen häufig verschieden. Die den in Frage stehenden Allelenkombinationen entsprechenden Wachsüberzüge können in ihrer Stärke nicht sämtlich okular unterschieden werden.

Wlo und *Wsp* sind für die Ausbildung von Wachs durch die *Wb*- und *Wa*-Allelenserien erforderlich. In ihrer rezessiven Form sind sie als lokale Inhibitoren, Hemmungsgene, des Wachsbildungsprozesses anzusprechen. *wlo* bedingt vollkommene Wachslosigkeit der Blättchenoberseite, *wsp* vollkommene Wachslosigkeit der übrigen Pflanzenteile. Die Kombination *wlo wsp* bedingt daher vollkommen wachslose Pflanzen, die phänotypisch von *bl*-Pflanzen nicht zu unterscheiden sein sollen. Kombinationen zwischen *bl* und *wlo* bzw. *wsp* konnten von mir mangels an Material noch nicht untersucht werden.

SUMMARY.

(1) The co-operation of the genes *Wb*, *Wlo* and *Wsp* for wax in *Pisum* was studied.

(2) It was found that *wlo* causes complete absence of wax on the upper side of the leaflets and that *wsp* produces the same condition on all other parts of the plant.

(3) The waxy parts of the plant have exactly the same wax intensity as is caused by the other genes for the development of wax (*Bl* and the multiple allelomorphs of *Wa* and *Wb*). Consequently, *wlo* and *wsp* have no influence on the formation of wax by these genes.

(4) Thus recessiveness in both *wlo* and *wsp* causes complete absence of wax in *Pisum*. These two genes can be considered as local inhibitors of the chemical process for formation of wax.

VII. TRAGANTFLECKEN ZWISCHEN KEIMBLÄTTERN UND TESTA SOWIE IHRE VERERBUNG.

In dem aus Kreuzungen stammenden Züchtungsmaterial von Weibullsholm wurden einigemale gelbsamige Individuen angetroffen, deren Samen orangefarbige Flecken hatten. Es gab stets nur zwei Flecken, die symmetrisch zu beiden Seiten nahe der Caruncula beginnen und sich nach rückwärts ausbreiten. Fig. 1 zeigt die Lage dieser Flecken im Verhältnis zu Hilum und Radikula. Die Ausbreitung dieser Flecken zeigt eine ziemlich starke Variation. Innerhalb einer Linie ist sie jedoch weniger veränderlich.

Eine solche Pflanze mit orangefleckigen Samen wurde u. a. 1936 in F_3 einer Kreuzung zwischen der Kocherbse Ambrosia I und der Kneifelerbse Extra Rapid angetroffen. Die Nachkommen dieser Pflanze verblieben in bezug auf diese Eigenschaft konstant und wurden im weiteren als Linie 379 geführt, die als Elter zu den unten zu besprechenden Kreuzungen verwendet worden ist.

Fig. 1. Links Same mit durch Rezessivität im Gen *tram* bedingten Tragantflecken; rechts Same mit dem *griseostriata*-Merkmal (das Gen *gri*).

Eine nähere Untersuchung der Samen von L. 379 ergab, dass die Flekken sich nicht in der Samenschale selbst befanden sondern dadurch bedingt wurden, dass die Samenschale an diesen Stellen durch ausgeschiedenen und erstarrten Pflanzenschleim mit den Keimblättern verklebt ist. An den übrigen Stellen befindet sich zwischen Testa und Kotyledonen eine Luftschicht, die den Erbsensamen eine weissgelbliche Farbe verleiht. Die beiden Flecken, an denen die Testa mit den Keimblättern verklebt ist, zeigen dagegen die lebhaft orangegelbe Farbe der letzteren.

Der eingetrocknete Pflanzenschleim scheint mit Tragant nahe verwandt zu sein. Er bildet wie letzterer eine durchscheinend klare Substanz, die in Wasser stark quillt. Da die Bezeichnung Tragant keine chemisch einheitliche Substanz angibt, sondern sich nur auf eingetrockneten Pflanzenschleim mit gewissen Eigenschaften (durch Wasser wieder in klaren Schleim umzuwandeln usw.) bezieht, habe ich es für berechtigt gehalten, die in Frage stehenden Flecken als Tragantflecken anzusprechen. Erwähnt sei in diesem Zusammenhang, dass

E. v. TSCHERMAK (1940) den die Verklebung der sog. Chenille-Samen von *Pisum* (bedingt durch das rezessive Gen *s*) verursachenden Stoff als Tragant auffasst. Das Gleiche soll auch für verklebte Samen von *Cicer* gelten. Echter Tragant ist der eingetrocknete Pflanzenschleim der Stämme von orientalischen *Astragalus*-Arten (*adscendens*, *brachycalyx*, *gummifer*, *microcephalus*, *pycnocladus*, *stromatodes*, *Kurdicus* und *verus*), also gleichfalls von Leguminosen produziert. Bei den sog. Chenille-Samen von *Pisum* wird der Pflanzenschleim auf der Aussenseite der Samenschale ausgeschieden, was zur Folge hat, dass die Samen während des Reifeprozesses miteinander verkleben. Voraussetzung ist hierbei natürlich, dass sie in der Hülse so nahe einander sitzen, dass sie während des Reifeprozesses miteinander in Berührung stehen.

Zur Feststellung der Vererbung der Tragantflecken wurden mit der oben genannten Linie 379 mehrere Kreuzungen ausgeführt, von denen unten drei besprochen werden.

Kreuzung Nr. 353; L. 232, de Winton × L. 379. L. 232 hat in bezug auf die Samen die genische Konstitution *A s f R I*, L. 379 entsprechend *a S F R I*. Die auf F_1 erhaltenen Samen waren demnach vom *A*-Typus, d. h. gefärbt. Im allgemeinen konnten auf diesen Samen (F_2) die orangegelben Flecken nicht gefunden werden, auf einzelnen konnten die Flecken jedoch zweifellos festgestellt werden. Die *A*-Samen dieser Kreuzung hatten jedoch eine verhältnismässig helle Grundfarbe, mit den durch *F* bedingten violetten Pünktchen. F_2 zeigte hinsichtlich Samenmerkmale folgende Spaltungen:

331 *A* : 88 *a*; D/m für 3 : 1 = — 1,89.
250 *F* : 81 *f*; » » » = — 0,22.
343 *S* : 76 *s*; » » » = — 3,27.

Die Spaltung in *S* : *s* zeigt das häufig vorkommende Defizit an *s*-Pflanzen, bedingt durch gleichzeitige Spaltung in bezug auf den Abstand zwischen den Samen in der Hülse und ev. Samengrösse, mit dem Ergebnis dass bei einem Teil der *s*-Pflanzen die Samen während des Reifeprozesses nicht miteinander in Berührung stehen und daher auch nicht miteinander verkleben.

Bei der Suche nach fleckigen Samen zeigte sich, wie auf Grund der F_1-Ergebnisse zu erwarten war, dass diese nur innerhalb der *a*-Gruppe (farblose Testa) mit Sicherheit erkannt werden konnten. Die 88 *a*-Individuen spalteten nach

63 ohne Flecken : 25 mit Flecken; D/m für 3 : 1 = + 0,74.

Das Merkmal orangegelbe Flecken der Samen ist demnach zweifellos als einfach rezessiv aufzufassen. Erwähnt sei in bezug auf diese Kreuzung noch, dass sie semisteril, d. h. annähernd 50 % fertil, war. Die Semisterilität zeigte jedoch in F_2 keinerlei Zusammenhang mit der Spaltung in Samenfleckigkeit.

Von Interesse ist in dieser Kreuzung ferner das bifaktorielle Spaltungsverhältnis in den beiden Merkmalen Chenille-Samen (*s*) und Fleckigkeit, da beide diese auf die Ausscheidung von Tragant zurückzuführen sind. Die 88 *a*-Samen konnten folgendermassen klassifiziert werden:

Gefunden:	60 *S* ohne Fl.	: 25 *S* mit Fl.	: 3 *s* ohne Fl.	: 0 *s* mit Fl.
Erwartet laut monohybr. Spaltg.	60,8 »	: 24,2 »	: 2,2 »	: 0,8 »
D/m für 9 : 3 : 3 : 1	— 0,17	+ 0,22	+ 0,22	— 0,35

Wie ersichtlich besteht in der *a*-Gruppe ein sehr starkes Defizit an *s*-Samen. Man könnte hier am ehesten geneigt sein an eine Koppelung zwischen *A* und *S* zu denken. Hierfür wurde in der vorliegenden Kreuzung erhalten:

Gefunden:	258 *A S*	: 73 *A s*	: 85 *a S*	: 3 *a s*
Erwartet laut monohybr. Spaltg.	270,9 »	: 60,1 »	: 72,1 »	: 13,9 »
D/m für 9 : 3 : 3 : 1	— 1,28	+ 1,61	+ 1,61	— 2,60

Die Möglichkeit dass *A* mit *S* gekoppelt ist, kann nicht abgewiesen werden. Da die Zahlen aber nicht signifikativ sind, besteht ebensogut die Möglichkeit, dass ein mit *a* gekoppeltes Gen für den Abstand der Samen in der Hülse (ev. Hülsenlänge oder Samengrösse) gleichzeitig spaltet und dadurch indirekt das Defizit an *s*-Pflanzen bedingt. Da die Spaltung eines solchen Gens in dieser Kreuzung durch das Defizit an *s*-Pflanzen überhaupt als erwiesen zu betrachten ist, halte ich diese letztere Erklärung für die wahrscheinlichere.

Die ev. Annahme eines physiologischen Hindernisses, dass die starke Tragantausscheidung an der Testaaussenseite der *s*-Samen eine weitere solche an der Innenseite derselben unmöglich bzw. selten realisierbar mache, erscheint nicht stichhältig, da dann wenigstens die *a s*-Pflanzen

ohne Flecken kein Defizit aufweisen sollten. Aber diese zeigten laut Obenstehendem relativ dasselbe Defizit. — Auf die Frage, ob die Tragantflecken durch Ausscheidung seitens der Samenschale oder der Keimblätter erfolgt, soll später bei Kr. 507 eingegangen werden.

Kreuzung Nr. 358; L. 234 × L. 379. L. 234 hat in bezug auf Samenmerkmale folgende genische Konstitution: *A Pl F Ast R I*. Die auf F_1 erhaltenen Samen zeigten in dieser Kreuzung bedeutend dunklere Samen als in Kr. 353. Diese dunklere Farbe wird zu grossem Teil durch das dominante Gen *Pl* bedingt. Auf diesen Samen konnte in keinem Fall auch nur eine Spur der orangegelben Flecken beobachtet werden. In F_2 wurde ein der vorigen Kreuzung entsprechendes Ergebnis erhalten, indem nur die *a*-Samen hinsichtlich der Flecken klassifiziert werden konnten. Es ergaben sich folgende Spaltungsverhältnisse:

247 *A* : 88 *a* ; D/m für 3 : 1 = + 0,53.
180 *Ast* : 67 *ast*; » » » = + 0,77.

Das Gen *Pl* bleibt hier unberücksichtigt, da es in F_2 dieser Kreuzung mit auftretender Spaltung in 50-, 66,6-%iger und normaler Fertilität Zusammenhang zeigte. Für die Spaltung in bezug auf Samenfleckigkeit (*a*-Pflanzen) ergab sich:

62 ohne Flecken : 24 mit Flecken; D/m für 3 : 1 = + 0,49.

Das Ergebnis dieser Kreuzung bestätigt nur das schon in der vorigen festgestellte, dass nämlich das Merkmal orangegelbe Flecken der Samen einfach rezessiv vererbt wird. Für das hier wirksame Gen soll, abgeleitet von *Tragant* und *maculatum* = gefleckt, das Symbol *tram* eingeführt werden.

Kreuzung Nr. 507; L. 379 × L. 458, Olympia II. L. 458, eine niedrige Brechmarkerbse, hat hinsichtlich Samenmerkmale folgende Genenformel: *a r i pl m ast S F*. Zum Unterschied von den vorstehenden Kreuzungen spaltet diese also nicht nach *A* : *a*. Von L. 379 unterscheidet sich L. 458 in *a r i* sowie im Fehlen der Flecken, wobei allerdings noch unklar war, ob und wie sich die Flecken auf den Samen mit grünen Kotyledonen zu erkennen geben werden.

Die F_1- und F_2-Samen dieser Kreuzung werden, da sie durchweg *a* sind, Aufschluss darüber geben können, ob die Ausscheidung der Tragantflecken von der Samenschale nach innen oder von den Keimblättern nach aussen stattfindet. Da wir schon ein Gen, *s*, kennen, das die Ausscheidung desselben Stoffes von der Testa nach aussen bedingt, ist von vornherein anzunehmen, dass das Gen *tram* wahrscheinlich die

fleckenförmige Tragantausscheidung der Testa nach innen verursacht. Trifft letzteres zu, so sollten F_1-Samen, da die Testa aus mütterlichem Gewebe besteht, je nach der Kreuzungsrichtung Flecken aufweisen oder nicht. Würde die Ausscheidung seitens der Kotyledonen erfolgen, so sollten die F_1-Samen, da beide Kreuzungsrichtungen zu Heterozygotie in *Tram* führen, durchweg gleich sein. Letzteres ist nicht eingetroffen, sondern bei Verwendung von L. 379 als ♀ zeigten die F_1-Samen Flecken, bei L. 458 als ♀ waren sie dagegen ohne solche. Durch diese Feststellung erscheint somit bewiesen, dass das rezessive Gen *tram* die Ausscheidung von Tragantflecken seitens der Samenschale nach innen veranlasst und mit den Keimblättern nichts zu tun hat.

Von den F_2-Samen (erhalten auf F_1-Pflanzen), die in *R* und *I* spalteten, zeigten die der Genkonstitution *RI* und *Ri* entsprechenden ab und zu ganz schwache Flecken, was besagt, dass das Gen *Tram* auch in heterozygoter Form eine schwache Wirkung haben kann. Diese ist jedoch weit verschieden von der von *tram tram* bedingten und, wie schon erwähnt, überhaupt nur hin und wieder auftretend.

In F_2 dieser Kreuzung wurden folgende Spaltungsverhältnisse beobachtet:

331 *R* : 74 *r* ; D/m für 3 : 1 = — 2,61.
279 *I* : 106 *i* ; » » » = + 1,14.
266 *Tram* : 119 *tram*; » » » = + 2,68.

Das letzte Verhältnis bezieht sich natürlich auf sämtliche, d. h. *R*- und *r*-Pflanzen. Was zuerst die *Ri*-Pflanzen (rund und grün) betrifft, so zeigten diese in bezug auf die Flecken klar monohybride Spaltung, nämlich 62 ohne Flecken : 26 mit Flecken. D/m für 3 : 1 = + 0,99. Die Flecken auf diesen Samen sind von saftgrüner Farbe und sehr leicht zu klassifizieren. Die Ausbreitung der Tragantflecken auf den *RI*- wie *Ri*-Samen dieser Kreuzung zeigte eine erhebliche Variation, von etwas geringerer Ausbreitung wie in Fig. 1 links bis zu etwa $^4/_5$ der Samenoberfläche einnehmend.

Von besonderem Interesse sind die *r*-Samen. Auf diesen waren die Flecken niemals mit voller Sicherheit festzustellen. In einigen wenigen Fällen scheinen sie vorzukommen, aber dann in geringerer Stärke als bei *R*-Samen und daher unsicher erscheinend. Nun wurde, wie unten gezeigt wird, zwischen den Genen *R* und *Tram* sichere Koppelung gefunden. Zur Erklärung des Fehlens der Flecken auf den *r*-Samen bestehen daher zwei Möglichkeiten. Entweder ist die Koppelung so stark, dass unter den 74 *r*-Pflanzen keine mit der Kombination *r tram*

erhalten worden sind, oder auch die Runzelung der *r*-Samen hat im Zusammenhang mit der sich an vielen Stellen bildenden Luftschicht zwischen Testa und Keimblättern zur Folge, dass die Flecken sich so schlecht ausbilden, dass sie auch an den *r tram*-Pflanzen nicht sicher zu erkennen sind.

Für die Spaltung in den beiden Genen *R* und *Tram* ergab sich indessen folgendes Verhältnis:

Gefunden:	192 *R Tram*	: 119 *R tram*	: 74 *r* $\binom{Tram}{tram}$
Erwartet:	216,56 »	: 72,19 »	: 96,25 »
D/m für 9 : 3 : 4	— 2,52	+ 6,11	— 2,62

Das Defizit an *r*-Samen ist hier ohne Interesse, da es durch die Wahl der zur Aussaat gelangten F_2-Samen bedingt wird. Der starke Überschuss an *R tram*-Individuen, entsprechend der einen Elternlinie Nr. 379, zeigt zweifellos eine starke Koppelung zwischen diesen beiden Genen an. Der Rekombinationswert dürfte für diese nur einige Prozent erreichen. Das Gen *Tram* sollte demnach zur Koppelungsgruppe *Pa R Tl Bt* gehören.

Zusammenfassend kann über die Wirkung des Gens *Tram* folgendes gesagt werden. *Tram* bedingt in seiner rezessiven Form auf der Innenseite der Samenschale die Ausscheidung von zwei symmetrisch zu beiden Seiten der Caruncula gelegenen Tragantflecken. Bei gelber Keimblattfarbe geben sich diese nach aussen durch lebhaft gelborange, bei grüner Keimblattfarbe durch saftgrüne Flecken zu erkennen. Das Gen *Tram* zeigt ziemlich starke Koppelung mit *R*. Da bisher keine sicheren *r tram*-Samen erhalten wurden, konnte bisher nicht entschieden werden, ob die Runzelung der *r*-Samen auch an sich die deutliche Ausbildung der Flecken verhindert.

SUMMARY.

(1) The author describes a new variety of *Pisum* with two symmetrical spots on the seed coat (see Fig. 1, to the left). These spots are caused by the secretion of a tragacanth-like substance on the inner side of the seed coat.

(2) With certainty these spots can be observed only on *a*-seeds, which have an uncoloured seed coat. On *a I*-seeds the spots are orange, on *a i*-seeds they are sap-green in colour. On *a r*-seed the presence of these spots has not hitherto been definitely established.

(3) The secretion of tragacanth on the inner side of the seed coat

is caused by recessiveness in a gene *tram* (from *tragacanth* and *maculatum*).

(4) The segregation in F_2 of a cross shows that *tram* is linked with the gene *r* for wrinkled seeds.

VIII. DAS TESTAMERKMAL GRISEOSTRIATA UND SEINE VERERBUNG.

Bei *Phaseolus vulgaris* wurde von mir (LAMPRECHT, 1932) ein als Mikropylenstreifen bezeichnetes Merkmal der Samenschale beschrieben. Dieser Streifen geht, wie der Name andeutet, von der Nähe der Mikropyle aus und reicht um das Ende der Bohne herum (l. c., Fig. 1). Mitunter ist er auch auf der ganzen, dem Hilum gegenüber gelegenen Seite deutlich ausgebildet. Er ist etwa $1\,^1/_2$ mm breit, von grauer Farbe und an seinen Seiten nicht scharf begrenzt, sondern diffus in die übrige Testafarbe übergehend. Je nach der Testafarbe erscheint auch der Streifen in verschiedenen Tönen. Das Merkmal Mikropylenstreifen hat sich bei *Phaseolus* als einfach (in einem Fall als doppelt) rezessiv bedingt herausgestellt.

Ein diesem Merkmal ganz ähnliches ist nun auch bei *Pisum sativum* wiederholt beobachtet worden. Fig. 1 rechts zeigt einen Erbsensamen mit diesem Merkmal. Der Streifen auf den Erbsensamen ist mehr oder weniger stark blassgrau, zuweilen nur schwach ausgebildet, gut 2 mm breit sowie gleichwie bei *Phaseolus* seitlich nicht scharf begrenzt sondern diffus erlöschend. Der Streifen beginnt kurz unterhalb der Radikula und reicht um den Samen herum bis fast zur Caruncula (der sternförmige Punkt in Fig. 1 rechts). Mit Sicherheit kann dieses Merkmal nur auf *a*-Samen festgestellt werden. Aber es gibt auch *A*-Samen (z. B. *m*, *pl*) mit helleren Farben, auf denen es deutlich zutagetritt.

Angetroffen wurde das *griseostriata*-Merkmal als Rezessivmutation teils in Linie 110 aus Kungserbse (aus Roi de Gourmands), teils in verschiedenen Kreuzungen. So hat die im vorigen Kapitel (VII) beschriebene L. 379 aus der Kreuzung Ambrosia I × Extra Rapid ausser den Tragantflecken auch das *griseostriata*-Merkmal. Eine weitere Linie, Nr. 450, mit dieser Eigenschaft stammt aus Kreuzung Nr. 72, L. 110 × L. 125 aus Pois Sabre. Ausserdem ist dieses Merkmal spontan in noch weiteren vier Kreuzungen aufgetreten. Die Pflanzen mit dieser Eigenschaft gaben diesbezüglich stets konstante Nachkommen. Im folgenden werden kurz die Ergebnisse von zwei Kreuzungen besprochen, in denen dieses Merkmal spaltete.

Kreuzung Nr. 341; L. 59 × L. 450. L. 59 hat in bezug auf Samenmerkmale folgende Konstitution: *A M f pl R I*, Linie 450 entsprechend *a m f pl R I* und überdies das *griseostriata*-Merkmal. Die auf den F_1-Pflanzen erhaltenen Samen zeigten dieses Merkmal nicht; es wäre aber wegen der dunklen Farbe derselben wahrscheinlich auch bei Vorhandensein nicht feststellbar gewesen. In F_2 wurden für die spaltenden Gene folgende Verhältnisse gefunden:

376 *A* : 104 *a* ; D/m für 3 : 1 = 1,68
359 *M* : 111 *m*; » » » = 0,95

Die *a*-Pflanzen spalteten ferner nach

71 ohne grauen Streifen : 23 mit grauem Streifen; D/m für 3 : 1 = = 1,58.

Das *griseostriata*-Merkmal ist demnach offenbar einfach rezessiv bedingt. Als Symbol für das hier spaltende Gen wähle ich, abgeleitet von *griseostriata*, *gri*.

Für die Zweigenenspaltungen ergaben sich folgende Verhältnisse:

Gefunden:	293	*A M* : 83	*A m* : 76	*a M* : 28	*a m*
Erwartet:	270,0	» : 90,0	» : 90,0	» : 30,0	»
D/m für 9 : 3 : 3 : 1	+2,11	— 0,82	— 1,64	— 0,38	

Gefunden:	44	*M Gri* : 32	*M gri* : 27	*m Gri* : 1	*m gri*
Erwartet laut monohybr. Spaltg.	51,9	» : 24,1	» : 19,1	» : 8,9	»
D/m für 9 : 3 : 3 : 1	— 1,56	+ 1,98	+ 1,98	— 3,19	

Das letzte Spaltungsverhältnis spricht für eine starke Koppelung zwischen *M* und *Gri*. Da die Zahlen jedoch ziemlich klein sind, will ich dieses Ergebnis einstweilen nicht als sicher auffassen.

Kreuzung Nr. 358; L. 234 × L. 379. Beide Elternlinien sind schon im vorigen Kapitel (VII) beschrieben worden. L. 379 wird, wie vorhin erwähnt, auch durch das rezessive Gen *gri* gekennzeichnet. An den auf F_1 erhaltenen Samen war auch hier nichts vom *griseostriata*-Merkmal zu erkennen. Die Samen hätten hierzu auch zu dunkle Farbe gehabt. F_2 zeigte folgende Spaltung:

66 *Gri* : 22 *gri*; D/m für 3 : 1 = 0,0,

also zufällig genau mit dem theoretischen Verhältnis übereinstimmend.

Von Genen, die an *a*-Samen sich manifestieren und daher gemeinsam mit der Spaltung in *Gri* : *gri* klassifiziert werden konnten, gab es

nur *Pl* und *Tram*. Es ergaben sich folgende bifaktorielle Spaltungsverhältnisse (die monofaktoriellen Verhältnisse waren 174 *Pl* : 42 *pl* und 64 *Tram* : 24 *tram*):

Gefunden:	31 *Pl Gri* : 18	*Pl gri* : 4	*pl Gri* : 1	*pl gri*
Erwartet laut monohybr. Spaltg.	31,7 »	: 17,3 »	: 3,3 »	: 1,7 »
D/m für 9 : 3 : 3 : 1	— 0,19	+ 0,24	+ 0,24	— 0,39

Gefunden:	49 *Tram Gri* : 15	*Tram gri* : 17	*tram Gri* : 7	*tram gri*
Erwartet:	49,5 »	: 16,5 »	: 16,5 »	: 5,5 »
D/m für 9 : 3 : 3 : 1	— 0,10	— 0,41	+ 0,13	+ 0,66

Die beiden Genpaare *Pl—Gri* und *Tram—Gri* scheinen unabhängig voneinander zu spalten; die Werte sind jedoch zu klein um auch nur einigermassen sichere Schlüsse zuzulassen.

Über das Testamerkmal *griseostriata* kann zusammenfassend gesagt werden, dass es durch das Gen *gri* in seiner rezessiven Form bedingt wird, dass die Manifestation dieses Gens im allgemeinen nur bei *a*-Samen festgestellt werden kann sowie dass *gri* wahrscheinlich mit *M* gekoppelt ist.

SUMMARY.

(1) The author describes a new character (*griseostriata*) of the seed coat of *Pisum*, a rather large, pale greyish stripe (see Fig. 1, to the right).

(2) A study of the inheritance of this character shows that it is conditioned by the recessive form of a gene, which the author indicates by the symbol *gri*. In F_2 a monohybrid segregation of the character mentioned has been ascertained.

(3) Probably the gene *Gri* shows strong linkage with *M* (marbled seeds).

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A PENTAPLOID F_1 HYBRID BETWEEN TWO DIPLOID POTENTILLA SPECIES

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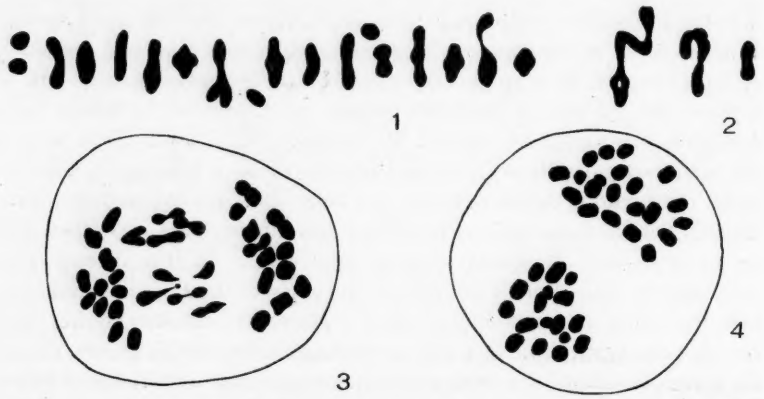
IN the *Potentilla* groups *Argenteae* and *Aureae vernalis* most species seem to be pseudogamous, as a rule giving only maternal offspring in intra- as well as inter-specific crosses. An exception to this rule is represented by the *P. argentea* strains A—C and A—G, which were described previously (A. and G. MÜNTZING, 1941). Both these strains are sexual or partially sexual, and with their help a number of true hybrids, representing different intra- and inter-specific combinations, were raised. One of these successful crosses has already been described, *viz.* the cross A—G × *P. opaca* (l.c., pp. 261—266). In this species cross both parents were diploid ($2n = 14$), and most of the F_1 plants evidently had the same chromosome number. However, meiotic studies also revealed the occurrence of a low proportion of triploid F_1 plants, resulting from the union of unreduced *argentea* gametes with reduced *opaca* gametes. The minimum percentage of triploids was found to be 4, the actual frequency probably being slightly higher. Morphologically the triploid F_1 plants were more similar to *P. argentea* than the diploid, intermediate hybrids. A certain group of F_1 plants, derived from the A—G plant 9—1—B as female parent, comprised 80 individuals. 79 of these plants were true hybrids, but the remaining plant (»164—1») was clearly deviating and apparently maternal (l.c., p. 262). It was supposed to be a product of an occasional pseudogamous seed formation or of an unsuccessful emasculation followed by self-fertilization. In the first year of observation this plant was not especially studied, but in the second year it attracted more attention, and fixations of the meiosis in the p.m.c. were made, various fixatives being used. At the same time the plant in question was found to be highly sterile, the percentage of good pollen being only 0—10 per cent. A rather large quantity of seeds of poor quality, derived from open pollination, were collected, but these seeds were not capable of germination and, thus, no progeny could be raised. The plant was much less vigorous than the luxuriating sister plants and died in the winter 1941—42. Afterwards, the meiotic fixations were studied and several rather satisfactory slides obtained.

Much to our surprise the plant under consideration proved to be pentaploid, having 34 or 35 chromosomes. This is evident from Figs. 1—4. Fig. 1 shows a I—M group in side view (separately drawn) with two clear trivalents, four univalents and apparently twelve bivalents. One of the latter bodies may in reality be a trivalent, and in that case the configuration is $3_{III} + 11_{II} + 4_I$. According to the first alternative the formula would be $2_{III} + 12_{II} + 4_I$. First metaphase was also ana-



Figs. 1—4. Meiosis in the p.m.c. of a pentaploid F_1 plant from the cross *Potentilla argentea* ($2n = 14$) × *P. opaca* ($2n = 14$). — Fig. 1, I—M in side view (separately drawn), $2_{III} + 12_{II} + 4_I$ or $3_{III} + 11_{II} + 4_I$; Fig. 2, two multivalents and a bivalent at I—M from the same cell; Fig. 3, I—A, showing the probable distribution 12—2 + 6/2—14; Fig. 4, II—M, probably representing 19 whole and 2 half chromosomes in one plate and 13 whole and 4 half chromosomes in the other plate. — × 4200.

lysed in nine other cells representing the following probable configurations: $1_V + 1_{IV} + 3_{III} + 6_{II} + 5_I$; $6_{III} + 3_{II} + 11_I$; $1_{IV} + 8_{III} + 3_{II} + 1_I$; $5_{III} + 8_{II} + 4_I$; $1_{IV} + 3_{III} + 8_{II} + 6_I$; $3_{III} + 10_{II} + 6_I$; $1_{IV} + 2_{III} + 10_{II} + 5_I$; $2_{III} + 12_{II} + 5_I$; $1_{IV} + 2_{III} + 9_{II} + 7_I$.

As the chromosomes are quite small, it is sometimes difficult to determine the exact number of chromosomes in the multivalents and sometimes even to distinguish between bivalents and trivalents. In the main, however, the configurations given reflect the true situation. Thus, in the plant 164—1 under consideration first metaphase is characterized by the presence of a high frequency of univalents and trivalents, and also larger associations occur. Fig. 2 shows two multivalents and a bivalent (to the right) from the same I—M group. At least the association to the left must be composed of more than three chromo-

somes. The frequency of univalents was determined in four different slides, the following total result being obtained:

Number of univalents:	0	1	2	3	4	5	6	7	...	11
Number of cells:	1	—	—	9	16	18	16	9	...	1

Thus, the number of univalents is seldom higher than 7 with an average of 5,01.

A typical I—A is represented by Fig. 3. The chromosome group to the left contains 12 chromosomes, the group to the right 14 chromosomes. Between the groups there seems to be six dividing univalents and two undivided chromosomes near the left group. This would make a total of 34 chromosomes. Another cell at I—A was found to contain 16 or 17 chromosomes in one of the anaphase groups, 15 chromosomes in the other one, and 3 dividing univalents between the groups. Fig. 4 shows the chromosome distribution in a cell at II—M. Both plates evidently contain undivided chromosomes as well as smaller bodies representing half univalents. In the upper plate there are probably 19 normal chromosomes and two half univalents, in the lower plate 13 undivided chromosomes and 4 half univalents. The cell given in Fig. 4 is unusually regular. Otherwise the cells at this stage frequently represented a rather irregular chromosome distribution and a high proportion of eliminated chromosomes.

The mode of meiosis in plant 164—1 is evidently rather similar to that in the pentaploid biotype of *Potentilla argentea* previously described (A. and G. MÜNTZING, 1941, pp. 248—251). This pentaploid *argentea*, however, seems to have a lower frequency of univalents than the present hybrid, the two average values being $3{,}92 \pm 0{,}15$ and $5{,}01 \pm 0{,}18$ respectively. The difference is $1{,}09 \pm 0{,}24$, giving a t of 4,54 and a $P < 0{,}001$.

The interesting point in the present case is the origin of a pentaploid F_1 hybrid from a cross between two diploid parents, having $2n = 14$. As mentioned above, most F_1 plants in the A—G $\times$ *opaca* cross were diploid, but a low proportion of triploid and more *argentea*-like F_1 hybrids also appeared. This demonstrates that some of the functional embryo-sacs in A—G are unreduced. Now, the only possible explanation of the present case is that in rare instances the A—G strain is also capable of producing functional embryo-sacs with twice the somatic chromosome number. Thus, the pentaploid F_1 hybrid must be derived from the union of a female gamete carrying 27 or 28 *argentea* chromosomes and a male gamete with 7 *opaca* chromosomes. The great preponderance of *argentea* chromosomes also explains the apparently maternal mor-

phology. A more detailed morphological study might have revealed the influence of the seven *opaca* chromosomes, but unfortunately the plant died before its constitution became known. It should also be observed that, owing to its sexuality, the A—G strain is in itself morphologically variable. This makes it more difficult to distinguish hybrids from true maternal plants.

In *Potentilla* fertilization of unreduced embryo-sacs has been established in several cases (A. and G. MÜNTZING, 1941, 1942; RUTISHAUSER, 1943 a and b; CHRISTOFF and PAPASOVA, 1943). The present case demonstrates that even embryo-sacs with twice the somatic chromosome number may function in the same way. Such cases have not previously been observed in *Potentilla* and, as far as we know, not in any other apomict either. However, a few cases are known from sexual species. Thus, in the hybridization experiments of SHIMOTOMAI (1933) *Chrysanthemum Makinoi* ($2n = 18$) was found to produce functional ovules with 36 chromosomes. These ovules, having twice the somatic number, gave viable hybrid zygotes when fertilized with pollen from *C. japonense* ($2n = 54$), *C. Decaisneanum* ($2n = 72$) and *C. pacificum* ($2n = 90$). Quite analogous results were obtained by NORDENSKIÖLD (1937) in crosses between diploid and hexaploid *Phleum* species. In diploid *Phleum nodosum* and *alpinum*, both having $2n = 14$, ovules with 7, 14 and 28 chromosomes are formed. The ovules with 28 chromosomes only function and give viable seeds in crosses with the hexaploid species *Phleum pratense* ($2n = 42$).

In *Chrysanthemum* and *Phleum* the ovules with twice the somatic number only give viable zygotes in crosses between species with widely different chromosome numbers. This has been attributed to the delicate 2 : 3 : 2 balance between the chromosome numbers of embryo, endosperm and somatic tissues (cf. MÜNTZING, 1936, p. 329). Evidently disturbances of this balance are less injurious in *Potentilla* than in several other genera. In the present case the union of gametes with 28 and 7 chromosomes, produced by two diploid species, gave a viable zygote. Nevertheless, a similar tendency as in *Phleum* and *Chrysanthemum* may also be traced in *Potentilla*. As already reported (A. and G. MÜNTZING, 1942), the diploid *P. argentea* strain A—C when crossed with other diploid *argentea* types gave only diploid hybrids ($2n = 14$). In crosses with hexaploid *argentea*, on the contrary, almost all the F_1 plants were pentaploid ($2n = 35$). In these crosses the reduced ovules are seldom fertilized or seldom give viable zygotes, the latter alternative being the more probable one. Viable seeds are almost exclusively ob-

tained from the union of unreduced ovules and reduced male gametes (14 + 21).

The sexual *argentea* strain A—G, used in the crosses with *P. opaca*, was also pollinated with pollen of hexaploid *argentea*. The total result was 16 diploid plants of maternal type, two plants having ± 35 and one

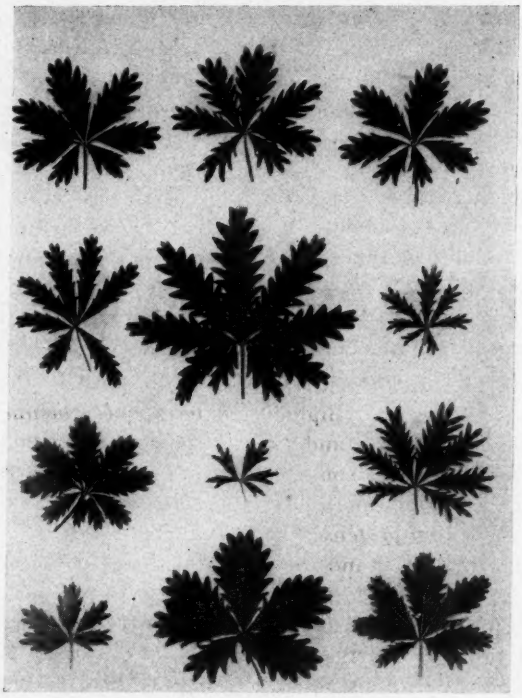


Fig. 5. Leaves of an *argentea* × *opaca* F_1 plant (upper row, 3 leaves) and its variable offspring (the three lower rows, leaves of 9 different plants).

plant with 2n = 43. Not a single plant had 2n = 28, the number to be expected from the union of reduced gametes of both parents. Thus, in this case the only viable zygotes, resulting from fertilization, were also derived from unreduced ovules or ovules with a still higher chromosome number. The plant with 2n = 43 must have been produced by an embryo-sac having 22 instead of 7 chromosomes. This is the second case in the A—G strain in which an ovule capable of fertilization was found to have more than the somatic chromosome number (14).

The ovule producing the pentaploid *argentea* × *opaca* hybrid had 27 or 28 chromosomes, twice the somatic number, in the second case 6 chromosomes were lacking.

P. argentea × *opaca*, F_2. — As already mentioned above, no progeny was obtained from the pentaploid F_1 plant. A number of other F_1 plants were isolated and seeds were also harvested after open pollination. In this way an F_2 generation consisting of a total of 96 full-grown individuals, derived from eight different mother plants, could be obtained. Only one of these plants was raised by isolation, all the others by open pollination. It is doubtful whether the latter plants are true F_2 plants. To a certain extent they may represent back crosses to the parents and other cross combinations. Be that as it may, the plants in question showed a very marked morphological variation (Fig. 5), thus demonstrating that the mother plants had all been entirely or predominantly sexual. A detailed morphological description of this F_2 is superfluous. It may be mentioned, however, that the number of leaflets as a rule ranged from 5 to 7, a few plants even having a higher number. In *P. argentea* the number is always 5, in *P. opaca* (= *P. heptaphylla*) generally 7.

The somatic chromosome numbers were determined in 83 of the F_2 plants. Of these, 77 had $2n = 14$, like the parents, one plant had $2n = 15$, one plant $2n = 20$, two plants $2n = 21$, one plant $2n = 24$, and one plant $2n = 35$. This variation demonstrates that most functional gametes in the F_1 plants were reduced, but that a proportion of unreduced ovules were also present, resulting in ± triploid offspring. The nature of the pentaploid F_2 plant remains uncertain, as the mother plant had been open-pollinated.

The percentage of good pollen in this F_2 material was estimated in 1942. At the same time pollen samples were taken from the corresponding mother plants. The following total results were obtained:

	Percentage of good pollen									
	0–10	10–20	20–30	30–40	40–50	50–60	60–70	70–80	80–90	90–100
6 F_2 progenies (total):	18	9	11	11	6	7	7	7	3	1
The corresponding mother plants:	1	4	1							

In the mother plants the percentage of good pollen ranged from 0 to 30, in the progenies from 0 to 100. Thus, in the offspring of the F_1 plants there was a very marked variation not only in morphology but also in pollen fertility. An average increase in pollen fertility is also quite clear.

P. opaca, a sexual species. — Of the parent strains used for the cross in question the *argentea* strain A—G is purely or predominantly sexual (A. and G. MÜNTZING, 1941, p. 257). On the other hand, preliminary observations seemed to indicate that the other parent, *P. opaca*, might be apomictic (l.c., p. 261). However, new progenies after open pollination of the *opaca* strains »Bäckaskog» and »Bjerred», raised in

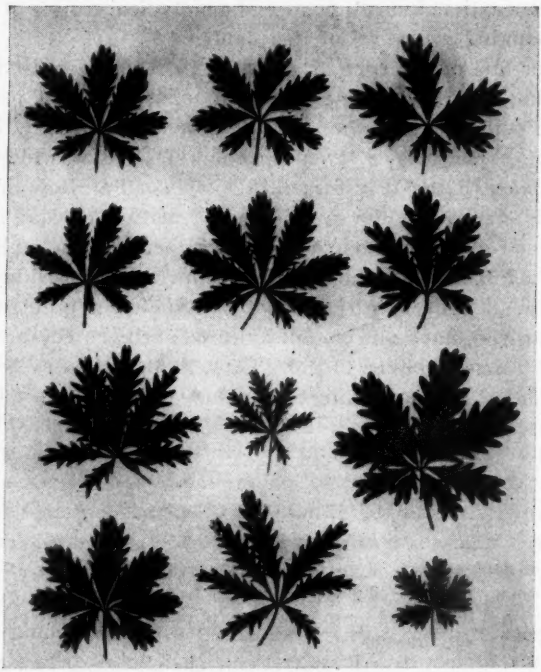


Fig. 6. Leaf shape variation in *P. opaca* (Bäckaskog). Upper row, 3 leaves of a certain mother plant; lower three rows, leaves of nine different daughter plants, representing morphological extremes.

1941, demonstrate that the species must be sexual. This time a rather marked morphological variation was apparent (cf. Fig. 6), being especially conspicuous with regard to leaf shape, anthocyanin colouring and flower dimensions.

The two progenies, which showed a clear average difference, *inter se* comprised each about 50 individuals. In both progenies pollen fertility was found to be variable, the percentage of good pollen ranging from 30 to 100 in the following way:

	Percentage of good pollen									
	30—40	—50	—60	—70	— 80	— 90	— 100	n	M
»Bjerred»:	1	1	4	2	6	14	24	52	83,7
»Bäckaskog»:		4	8	4	5	14	19	54	78,7

In 37 cases two pollen samples were taken from the same plant. These samples were taken on different days but showed a quite pronounced correspondence, thus indicating special genotypical causes of the pollen sterility occurring in several of the plants.

Another line of evidence of sexuality in *P. opaca* was obtained in the following way: As female parent *P. opaca* did not produce any seeds when pollinated with pollen of *P. argentea* (A. and G. MÜNTZING, 1941, p. 261). However, a low proportion of seeds was obtained from the cross *opaca* (Bjerred) × (*argentea* × *opaca*) F_1. Now, if the *opaca* ovules were fertilized by the F_1 pollen, representing a strong genotypical variation, the resulting progeny should be rather variable. The expected result was obtained in a small progeny comprising 7 individuals. These plants were all very *opaca*-like but represented a quite obvious segregation in leaf shape and anthocyanin colouring. The percentage of good pollen ranged from 50 to 100. Thus, though more evidence should be accumulated, it seems safe to conclude that *P. opaca* is a sexual species, at least the strains so far studied.

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DIE CHROMOSOMENPAARUNG VON ZWEI SALIX-BASTARDEN

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DIE Gattung *Salix* hat bekanntlich n = 19 Chromosomen mit di-, tetra-, hexa- und octoploiden Arten. Der Verfasser hat die Paarung von *Salix*-Chromosomen verschiedener Bastarde studiert, die alle von Professor NILS HERIBERT NILSSON, Lund, künstlich hergestellt worden sind. Der Verlauf dieser Paarung ergab sich deutlich schon bei Untersuchung des Bastardes *viminalis* × *caprea* (HÅKANSSON, 1929): F_1 und diploide Sträucher aus F_2 hatten 19 II und eine regelmässige Meiosis, triploide männliche wie weibliche Sträucher der F_2 hatten stets eine wechselnde Anzahl von Univalenten und im Zusammenhang hiermit gestörte Meiosis (s. auch HÅKANSSON, 1938). Theoretisch sollten die letzteren 19 III gehabt haben, aber ein Teil der III war immer in II und I aufgeteilt.

Die Chromosomenpaarung anderer *Salix*-Bastarde zeigen ähnliche Verhältnisse (HÅKANSSON, 1938). Enthält der Bastard eine gerade Anzahl Genome, so herrscht vollständige Paarung, während eine ungerade Anzahl von Genomen zu mehr oder weniger starker Univalentbildung und dadurch bedingten Störungen der Teilungen führt. So haben die diploiden Bastarde *purpurea* × *hastata*, *aurita* × *hastata*, *repens* × *viminalis*, *viminalis* × *aurita*, *viminalis* × *daphnoides* alle 19 II, was auch mit (*purpurea* × *daphnoides*) × (*repens* × *aurita*) der Fall ist. Tetraploide Bastarde mit im allgemeinen 38 II und sehr regelmässiger Meiosis waren *viminalis* (n = 19) × *phylicifolia* (n = 57) und der sog. *S. polygena*, den HERIBERT NILSSON durch Kreuzung von 8 verschiedenen Arten dargestellt hat. Hexaploid mit 57 II war *nigricans* × *phylicifolia*. Untersuchte Bastarde mit einer ungeraden Anzahl Genome sind vor allem mehrere triploide *cinerea*-Bastarde, die eine höhere Frequenz von I zeigten als die triploiden *viminalis* × *caprea*-Sträucher (jedoch nicht mehr als 19) und ferner der pentaploide *cinerea* × *phylicifolia*-Bastard.

Die Ergebnisse dieser Untersuchungen sprechen stark dafür, dass die in den verschiedenen Arten vorhandenen Genome zytologisch einander sehr ähnlich sind. Die zwischen ihnen vorhandenen Unterschiede

sind genischer Natur. Der Verfasser hat nun als Ergänzung zu früheren Untersuchungen noch zwei der von HERIBERT NILSSON dargestellten Bastarde studiert, nämlich einen mit ausserordentlich starker Sterilität und einen, der durch Kreuzung von Arten verschiedener Sektionen der Gattung dargestellt worden ist. Alle zur Bastardierung benutzten Arten sind diploid. Es wurde weibliche Sträucher untersucht.

S. lapponum × *hastata.* — Dieser Bastard ist in Skandinavien wildwachsend nicht angetroffen worden (FLODERUS, 1931). Laut mir zur Verfügung gestellten Angaben von HERIBERT NILSSON ist er nicht besonders schwierig darzustellen. Dagegen ist er sehr schwach wachsend und ausserordentlich steril. Zahlreiche Bestäubungsversuche haben nur zu wenigen reifen Samen geführt. Die Sträucher hatten zahlreiche Kätzchen.

Die Meiosis war auch hier vollkommen normal. In den EMZ wurden in den — ziemlich wenigen — Stadien der Metaphase 1 stets 19 II beobachtet. Die Teilungen waren regelmässig und führten zur Bildung von vier Makrosporen. Eine Verspätung der Meiosis fand nicht statt.

Aus diesen Beobachtungen geht also hervor, dass die starke Sterilität nicht durch chromosomale Störungen bedingt wird. Auch eine Entwicklungshemmung, die sich in starker Verspätung der Meiosis in den EMZ dokumentiert, ist nicht die Ursache. Letzteres war für die *cinerea*-Bastarde kennzeichnend, bei denen die Meiosis in einem Zeitpunkt stattfand, wo die Samenanlage einen fertigen Embryosack enthalten haben sollte (HÅKANSSON, 1938). Ferner zeigen die bisherigen Untersuchungen, dass die folgenden Arten ein zytologisch einander sehr ähnliches Genom haben: *lapponum, hastata, purpurea, aurita, viminalis, caprea, repens* und *daphnoides.* Berücksichtigt man ferner die Paarungsverhältnisse in den oben genannten *phylicifolia*-Bastarden, so wird klar, dass wenigstens ein Genom der hexaploiden Arten *phylicifolia* und *nigricans* ganz mit dem dieser diploiden Arten übereinstimmt. Die übrigen Genome der Hexaploiden sind untereinander ganz gleich. Wahrscheinlich ist indessen, dass sie auch mit dem ersten übereinstimmen, sodass alle diese Genome strukturell gleich sind. In bezug auf *cinerea* ist offenbar, dass das eine Genom dieser tetraploiden Art zur gleichen Gruppe gehört, während in bezug auf das andere einige Zweifel bestehen (s. HÅKANSSON, 1938). Bedingt werden diese Zweifel durch die beobachtete starke Univalentbildung in den triploiden *cinerea*-Bastarden. Es sei jedoch hervorgehoben, dass HERIBERT NILSSON einen *cinerea*-ähnlichen Strauch aus der Kreuzung *viminalis* × *caprea* erhalten hat (NILSSON, 1931).

S. viminalis × *triandra.* — Dieser Bastard ist aus der Natur bekannt (FLODERUS). *S. triandra* gehört zur Sektion *Amerina*, die von den Salicologen stets als von allen anderen *Salices* stark verschieden aufgefasst worden ist. Alle oben erwähnten Arten gehören dagegen zur Sektion *Caprisalix*. Es ist demnach der erste Sektionsbastard, von dem Meiosisstadien erhalten worden sind. Die Paarung zeigte sich auch hier von der bei den übrigen diploiden Bastarden abweichend. Die Chromosomenzahl betrug 38, aber 19 II wurden in EMZ niemals beobachtet. Die Paarung war stets unvollständig, es gab immer eine Anzahl von Univalenten. Der Grad der Paarung ist wegen der geringen Grösse der Chromosomen schwer feststellbar. Es ist häufig unsicher, ob man zwei I vor sich hat oder ein II mit unregelmässiger Lage in der Äquatorialebene oder mit grossem Abstand zwischen den zwei Homologen. Die Platte ist recht unregelmässig und die Anzahl Univalente nimmt gegen die Anaphase 1 zu, was gleichfalls das Feststellen des Konjugationsgrades erschwert. Es gab jedoch auch deutliche Bilder. Die Anzahl II variierte von 9—14, die der I von 10—20. Fig. 1 zeigt die Paarung in einer EMZ, in der die Platte der Metaphase 1 noch nicht fertig ist. Man sieht 9 II und 20 I.

Fig. 1. *Salix viminalis* × *triandra.* — 9 II + + 20 I.

Da die Fixierungen bei normalen äusseren Verhältnissen ausgeführt worden sind, kann die geschwächte Paarung nicht auf extreme äussere Bedingungen zurückzuführen sein sondern muss auf Unterschieden zwischen den *triandra*- und *viminalis*-Genomen beruhen. Das *triandra*-Genom ist damit auch von allen anderen hier besprochenen Genomen abweichend. Dies beruht sicherlich darauf, dass die Art der Sektion *Amerina* angehört. Die Auffassung der Systematiker wird demnach auch durch die zytologische Untersuchung bestätigt. Es bestehen nicht nur morphologische Unterschiede zwischen den Sektionen sondern auch bedeutende Unterschiede zwischen ihren Genomen.

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ABSTRACTS — KURZE MITTEILUNGEN

ARTUR HÅKANSSON: Eine »homozygotische» interspezifische Translokation.

Vor kurzem wurde ein Fall von interspezifischer Translokation bei *Godetia* entdeckt (HÅKANSSON, 1943). Aus Kreuzungen zwischen *G. deflexa* und *Whitneyi* hat Dozent G. HIORTH einen rotnervigen Typus erhalten, der die Rotnervigkeit trotz der Dominanz dieser Eigenschaft nur zu einem geringen Prozent vererbt. Dieser Typus hat 15 Chromosomen, nämlich 14 von *Whitneyi* und eines von *deflexa*. Letzteres tritt als Univalent auf und wird während der Meiosis häufig eliminiert. Dies dürfte die wichtigste Ursache des grossen Defizites an rotnervigen Pflanzen sein. Nach Bestäubung mit vorher röntgenbehandeltem Pollen wurde aus dem 15-chromosomigen Typus ein neuer rotnerviger Typus erhalten, der nach Selbstung annähernd 50 % rotnervige Individuen gibt (HIORTH, 1943). Diesem fehlten gewisse trisomische Eigenschaften, die der erste Typus aufwies, und er hatte auch nur 14 Chromosomen, die 7 Bivalente bildeten. Aus dem Aussehen eines der Bivalente ergab sich, dass ein Stück des *deflexa*-Chromosoms an das Ende eines *Whitneyi*-Chromosoms transloziert worden war.

Bei Veröffentlichung der vorigen Mitteilung war es noch unbekannt, ob der neue Typus homozygot rotnervige Individuen (*RR*) abspalten wird. Dies tat der alte Typus ja nicht; diese sollten dort »Tetrasomen» gewesen sein, die wohl kaum vital sind. Es hat sich nun gezeigt, dass der neue Typus wirklich Homozygoten gibt, die fast normalem Aussehen haben. Fünf solche Pflanzen sind zytologisch untersucht worden. Sie hatten alle 7 II. Multivalente wurden niemals beobachtet. Die gefundenen Paarungsverhältnisse entsprechen der Erwartung.

Gleichwie die Heterozygoten bildeten auch die Homozygoten ein in bezug auf das Fixieren schlechtes Material. Ein heteromorphes Bivalent gab es hier natürlich nicht, aber es war in der Regel nicht möglich ein Bivalent festzustellen, das aus den zwei Chromosomen mit Translokation gebildet sein musste. Das Translokationsbivalent konnte demnach nicht mit Sicherheit wiedererkannt werden.

Ganz regelmässig waren jedoch die meiotischen Teilungen der Homozygoten nicht. Eine recht deutliche Asyndese war zweifellos vorhanden. Etwa 15 % der Pollenmutterzellen zeigten 6 II + 2 I. Die beiden Univalente lagen in oder nahe der Äquatorialebene. Eine Elimination eines der beiden Univalente konnte vorkommen, was zu dem bekannten Bild von überzähligen Kernspindeln während der 2. Teilung führte. Dass so überwiegend nur 2 Univalente vorkommen, deutet darauf hin, dass die Chiasmafrequenz in einem bestimmten Bivalent herabgesetzt ist und es sollte demnach eine gewisse Wahrscheinlichkeit dafür bestehen, dass das Translokationsbivalent eine geringere Chiasmafrequenz aufweist als gewöhnliche Bivalente.

Hier liegt also die Erscheinung vor, dass ein Stück eines Chromosoms einer Art dem Genom einer anderen Art dauernd einverleibt worden ist. Von gewisser Bedeutung ist hierbei, dass *G. Whitneyi* und *deflexa* nicht näher miteinander verwandt sind; ihre Chromosomen können sich gar nicht mit-

einander paaren. Beim neuen Typus kommt es daher während der Meiosis zu keinen Komplikationen auf Grund von Multivalentbildung. Dagegen bedingt die Translokation offenbar eine gewisse Asyndese, was eine jedoch schwache Sterilität zur Folge haben dürfte.

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